5
P5

ABUNDANCE AND MORTALITY OF ANCHOVY EGGS CAUSED BY CANNIBALISM AND INTRAGUILD PREDATION, AND THE POTENTIAL EFFECT ON ANCHOVY RECRUITMENT AND CLUPEOID FLUCTUATIONS

by Edy Sylvia Valdes Szeinfeld

[RODRIGUEZ]

Supervisor: Prof C. L. Griffiths

Submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy at the University of Cape Town

To the memory of my parents which always accompanies me and to David (my husband), for his support, gratifying confidence in times of stress and constant encouragement all which made the Ph D thesis possible.

TABLE OF CONTENTS

DECLARATION

I hereby declare that unless otherwise stated this thesis represents my own work, both in concept and execution. The data collection was carried out during cruises mainly organized to estimate biomass of anchovy spawners. I participated in all of these cruises as a researcher. I had complete responsibility for all sampling and analysis of clupeoid diets to estimate cannibalism and predation. Sampling of ichthyoplankton and sorting for anchovy eggs were undertaken by a technical team over the years in consideration. Chapter three is a co-authored paper submitted for the Proceedings of the Symposium on "Trophic Functioning of the Benguela System"; held in Cape Town between 22-25 August, 1989 and organized by the Benguela Ecology Programme and the Foundation for Research Development. I carried out most of the anchovy diet component and determination of the feeding periods, and had minor input in the rest of the paper. In all other respects I lay claim to uncited ideas, concepts, hypotheses or conclusions contained in this thesis.

Signed by candidate

Signature Removed

Edy Sylvia Valdes Szeinfeld

31/10/1990

Date

ABSTRACT

This thesis is structured in the form of five main chapters, each written in the form of an independent paper and supported by a general conclusion and one previously published paper on the same general theme. The central theme is the dynamics, ecology and evolution of intraspecific and intraguild predation -specifically the determination of an interacting mechanism between the guild fish species *Engraulis capensis* and *Sardinops ocellatus* and its significance for future fisheries management.

Briefly the different chapters of the thesis are as follows:

Chapter 1: "Fecundity of the Cape anchovy, *Engraulis capensis*", provides qualitative and quantitative information on the interannual egg production by anchovy over the period 1986 to 1988. Interannual variation of batch fecundity and spawning fraction is studied looking for compensatory mechanisms of stock size changes. Because the stock size of Cape anchovy seems to have decreased considerably from 1986 to 1988, and average batch fecundity estimated at peak spawning time was about the same over the three years, a compensatory mechanism between batch fecundity and stock size was not detectable.

Chapter 2: "Abundance of clupeoid eggs in the Benguela Ecosystem and recruitment of anchovy *Engraulis capensis*" postulates an hypothesis about the impact of intraspecific (cannibalism) and

interspecific (intraguild predation by sardine) mechanisms on anchovy eggs. The relative importance of these two mortality factors as density-dependent mechanisms to anchovy recruitment is examined with respect to different concentration coefficients and indices of overlapping between potential predator and prey. The output of the model shows that the anchovy population appears as a saturated population when the index of overlapping is constant and is highly concentrated, or when potential predators are highly concentrated, producing poor recruitments. According to the model, a decrease in concentration indices for anchovy and sardine and a decrease of the overlapping index may lead to either a decrease or an increase in the abundance of eggs, depending on the sardine biomass and hence on the relative importance of intraguild predation and intraspecific predation on anchovy eggs at the time.

Chapter 3: "Estimates of the annual consumption of food by anchovy and other pelagic fish species off South Africa during the period 1984-1988" is co-authored by M. J. Armstrong, A.G. James and E. S. Valdes and has been submitted to the Proceedings of the Symposium on "Trophic Functioning of the Benguela System", held in Cape Town from 22 to 25 August, 1989. It provides information on abundance, diet and food consumption rate of anchovy *Engraulis capensis*. Separate estimates are made of the quantities of phytoplankton and micro-, meso- and macro-zooplankton consumed by the anchovy population off the West and South Coasts. These data are subsequently included in a network analyses of carbon flow through the foodweb of the Southern Benguela system reported by

Cochrane *et al.* and submitted to same Proceedings. The principal finding of this paper is that an assemblage of some 4 million tons (wet mass) of pelagic and mesopelagic fish occurring over the continental shelf of South Africa may have an annual consumption of approximately 3.5 million tons of carbon, over 90% of which is likely to be derived from meso- and macro-zooplankton eaten in roughly equal proportions.

Chapter 4: "The energetics and evolution of intraspecific predation in the anchovy, *Engraulis capensis*", provides information on the daily feeding period of the anchovy and about the energetics of feeding on their own eggs relative to alternative diets. The population energetics gain of this habit and the evolutionary consequences of this behaviour are discussed. Anchovy are found to have two peak feeding periods daily: one smaller one between 07h00 and 09h00, and a more pronounced one between 17h00 and 19h00. Anchovy consume, on average, 3.75 % body weight in order to support annual costs of reproduction and growth. However, this amount would vary according to which of a variety of energetically equivalent potential diets is consumed. Thus if anchovy fed exclusively on phytoplankton, equivalent energy input would require the equivalent of 5.8 % of body weight per day, while those feeding on zooplankton would need 3.5 - 4.5 % body weight, and fish feeding on their own eggs only 2.5 % body weight daily. Feeding on eggs at peak spawning on the spawning grounds -where there is a limitation of alternative food particles, i.e. zooplankton- seems adequate to support reproduction. The thermodynamic implication of egg consumption as an

energy regulating mechanism at a time of great energy expenditure is to maintain calories within a population but at the expense of negative entropy. This, decreases the ecological efficiency of secondary production and poses difficulties for an operational concept of a trophic level. In selection at the population level, cannibalistic fish benefit from homeostatic self-regulation.

Chapter 5: "Cannibalism and intraguild predation in clupeoids" provides empirical data obtained from 1986 to 1988 to test the hypothesis postulated in chapter 2. Actual rates of cannibalism and sardine predation on anchovy eggs, together with egg production estimates for those years, provide estimates of the percentages of anchovy egg mortality inflicted by cannibalism and sardine predation, giving support for the real impact of those density-dependent mechanisms on egg survival and thus, anchovy recruitment. Up to 56% of the total anchovy egg mortality was caused by predation by sardine and up to 6% by cannibalism over the period studied. Although the proportion of the egg mortality caused by cannibalism might seem too low to cause a dome-shaped stock-recruitment, its density-dependent nature may cause -on average- 70% of the total egg mortality at places of high egg density. Therefore, when the anchovy egg density is high and there is no competitive mortality due to intraguild predation the effect of cannibalism is likely to be greater.

Chapter 6: "General discussion and conclusions" is an integrated report of the previous chapters, highlighting the importance of the

identification of these intra-specific and inter-specific mechanisms on anchovy recruitment, the application of the Ricker's model, the interaction of guild species and the possible implications for multi-species management of sardine and anchovy resources. The ecological consequences of both mechanisms at different levels and their connotations in an evolutionary perspective are also discussed.

Appendix I is included as a supporting paper. It provides information about observations on cannibalism made during 1984 and 1985, prior to registration for the Ph D degree, but upon which I based the hypothesis developed in chapter 2.

C H A P T E R 1

FECUNDITY OF THE CAPE ANCHOVY *Engraulis capensis*

Edy S. Valdes

Sea Fisheries Research Institute, Private Bag X2, 8012 Rogge Bay, South Africa.

Key words: *Engraulis capensis*, anchovy, fecundity, South Africa.

ABSTRACT

The Cape anchovy (*Engraulis capensis*) is a serial spawner releasing several batches of eggs each spawning season. Batch fecundity from 1986 to 1988 was estimated and its inter-annual variation investigated. Relative fecundity, estimated for November 1986 (542 eggs g^{-1} female), November of 1987 (582 eggs g^{-1} female) and November of 1988 (614 eggs g^{-1} female), did not show significant interannual variation nor any regional differences. The frequency of spawning at peak spawning varied between 0.080 and 0.095 with a mean of 0.086. Therefore, on average, anchovies spawned a new batch of eggs every 12 days. Because the stock size of Cape anchovy seems to have decreased considerably from 1986 to 1988, and batch fecundity estimated at peak spawning time was about the same over the three years, a compensatory mechanism between batch fecundity and stock size was not detectable.

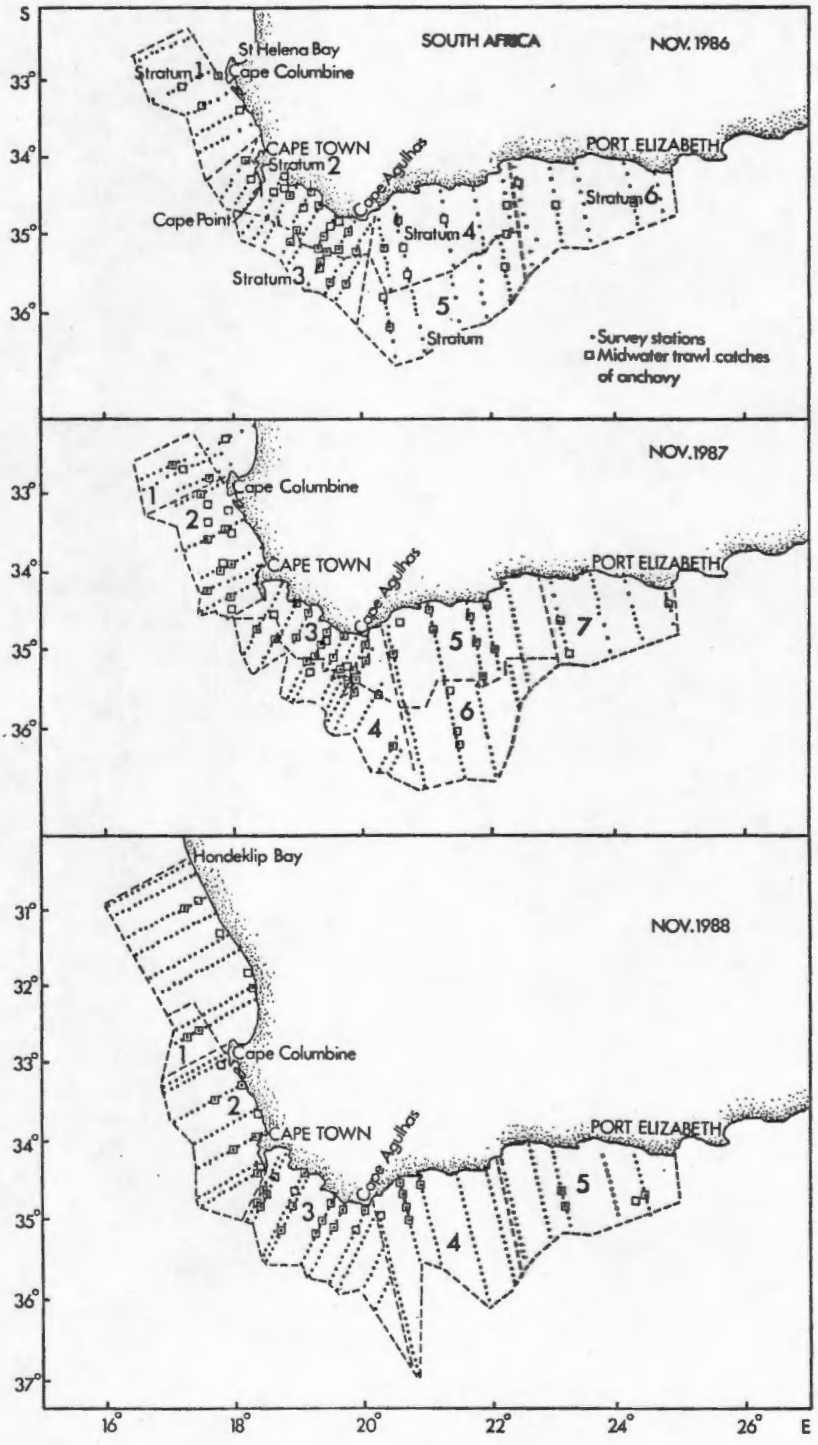
I. INTRODUCTION

The annual fecundity of anchovy (*Engraulis*) species is a function of both batch fecundity (the number of eggs released by a mature female in a single spawning event) and spawning frequency (the number of times each female spawns per year). Batch fecundity in northern (*Californian*) anchovy *Engraulis mordax* has been studied by Hunter and Golberg (1980), and in the Peruvian anchovy *E. ringens* by Alheit and Alegre (1986). They used the "Hydrated Oocytes Method" (Hunter *et al.* 1985) to estimate batch fecundity. The Cape anchovy is a serial spawning clupeoid, releasing several batches of eggs per year (Armstrong *et. al.* 1988) like the northern and Peruvian anchovies (Hunter & Golberg, 1980, 1981; Alheit et al. 1984). Interannual variation in spawning frequency (based on data from Armstrong *et. al. 1988* and Sea Fisheries Research Institute, SFRI, unpubl.) and batch fecundity for the period 1986 to 1988 are reported below.

II. MATERIALS AND METHODS

Surveys were conducted aboard the research ship *Africana* during November of 1986, 1987 and 1988 to coincide with peak anchovy spawning (Armstrong *et al.* 1988). Anchovy were collected around the South African coast (Fig. 1) on a sample grid which normally did not extend farther north than Cape Columbine on the west coast, or farther east than Port Elizabeth on the south coast.

Fig. 1 : Map of the South African coastline showing survey designs, positions of survey stations and positive trawl for anchovy catches for the three years, 1986-1988.



Samples were collected using an Engels-308 midwater trawl with an 8-mm cod-end liner.

Batch fecundity could not be estimated for each trawl station because of the small proportion of trawls containing hydrated females. During the 1986, 1987 and 1988 surveys 81, 81 and 102 females with gonads that were hydrated, but had not yet ovulated, were collected respectively and preserved in 10% buffered formalin. In the laboratory the weight of the fish minus its ovary (ovary-free weight) and of the ovary were determined. Three tissue samples of about 50 mg were taken from each ovary. The number of hydrated oocytes in each of these subsamples was counted. Hydrated oocytes could be distinguished easily from other oocytes by their large size, wrinkled appearance and translucence. The total number of hydrated oocytes in the ovaries, which corresponds to the batch fecundity, was calculated for each female from the number of hydrated oocytes per subsample and the total ovary weight.

Batch fecundity was calculated from the total samples of hydrated females and expressed as a linear function of ovary-free wet weight of females. The linear regression allowed the population mean batch fecundity to be predicted from the mean female mass, with a suitable adjustment for the discrepancy between the mass of live and preserved specimens. To do this, the estimate of mean weight was divided by the factor 1.0224 to adjust for a predicted 2-7 % increase in mass after 60 days in 10 % formalin (Hunter, 1985) and

for the removal of the ovaries, which prior to hydration were determined to weigh on average 5 % of the ovary-free live mass in the most abundant size class of females, as indicated in Armstrong *et al.* (1988).

Relative fecundity was expressed as number of eggs spawned (batch fecundity) divided by the ovary-free female weight. The gonadosomatic index (GSI) was determined by dividing the ovary weight by the ovary-free female weight and expressed as a percentage.

In order to investigate possible regional differences in fecundity, relative fecundity was calculated for females caught in different areas. Three areas were considered:

i) West-coast from off Cape Point to off Cape Columbine except in 1988, when the survey extended to Hondeklip Bay. Along the west coast area, the recruitment of 0-year-old anchovy takes place from mid-autumn onwards and is initially strongest to the north of St. Helena Bay (Crawford *et al.* 1983)

ii) South-west coast from Cape Point to Cape Agulhas, the main spawning ground for anchovy as indicated by density of eggs and fish (Armstrong *et al.* 1988)

iii) South-east coast from Cape Agulhas to Port Elizabeth, the eastern region of the Agulhas Bank, where two-year-old and

older anchovies predominate (Armstrong *et al.* 1988).

III. RESULTS

The spawning fraction (S) varied between 0.080 and 0.095 with a mean of 0.086 (Table I). Therefore, on average, anchovies spawned a new batch of eggs every 11.63 days during the peak of the spawning season.

The relationships between batch fecundity and ovary-free mass of preserved females are illustrated in Fig. 2. Parameters estimated for the straight-line regressions are listed in Table II. The mean weight of females was 11.70 g in 1986 (Armstrong *et al.* 1988) and 11.06 g and 12.02 g in 1987 and 1988 respectively (SFRI, unpubl.). Batch fecundity (F) was highest in 1987 at 6490 eggs per female (Table II). However, there was no statistically significant difference ($P>0.1$) between the three years. Furthermore, there was no significant difference ($P>0.3$) between the mean relative fecundity of females (RF) in 1986 (542 eggs g^{-1}, n=81, range= 174-2488, 9.0-13.0 cm SL), 1987 (582 eggs g^{-1}, n=81,range=154-1012, 9.5-13.5 cm SL) and 1988 (614 eggs g^{-1}, n=102, range=115-1272, 9.5-14.5 cm SL) (Table II).

Table I: Estimated spawning fraction per day (S), variances ($V = \hat{\mu} \times 10^{-3}$) and number of samples (N) for anchovy sampled off South Africa during 1986-1988 (sources: Armstrong *et. al.* 1988 and SFRI unpubl.).

Year		
1986	1987	1988
S 0.095	0.080	0.084
V 45.9	14.2	15.1
N 997	1552	1101

Fig. 2 : Regressions of batch fecundity against ovary-free mass of preserved female anchovy in November 1986, 1987 and 1988 (see table II for regression parameters).

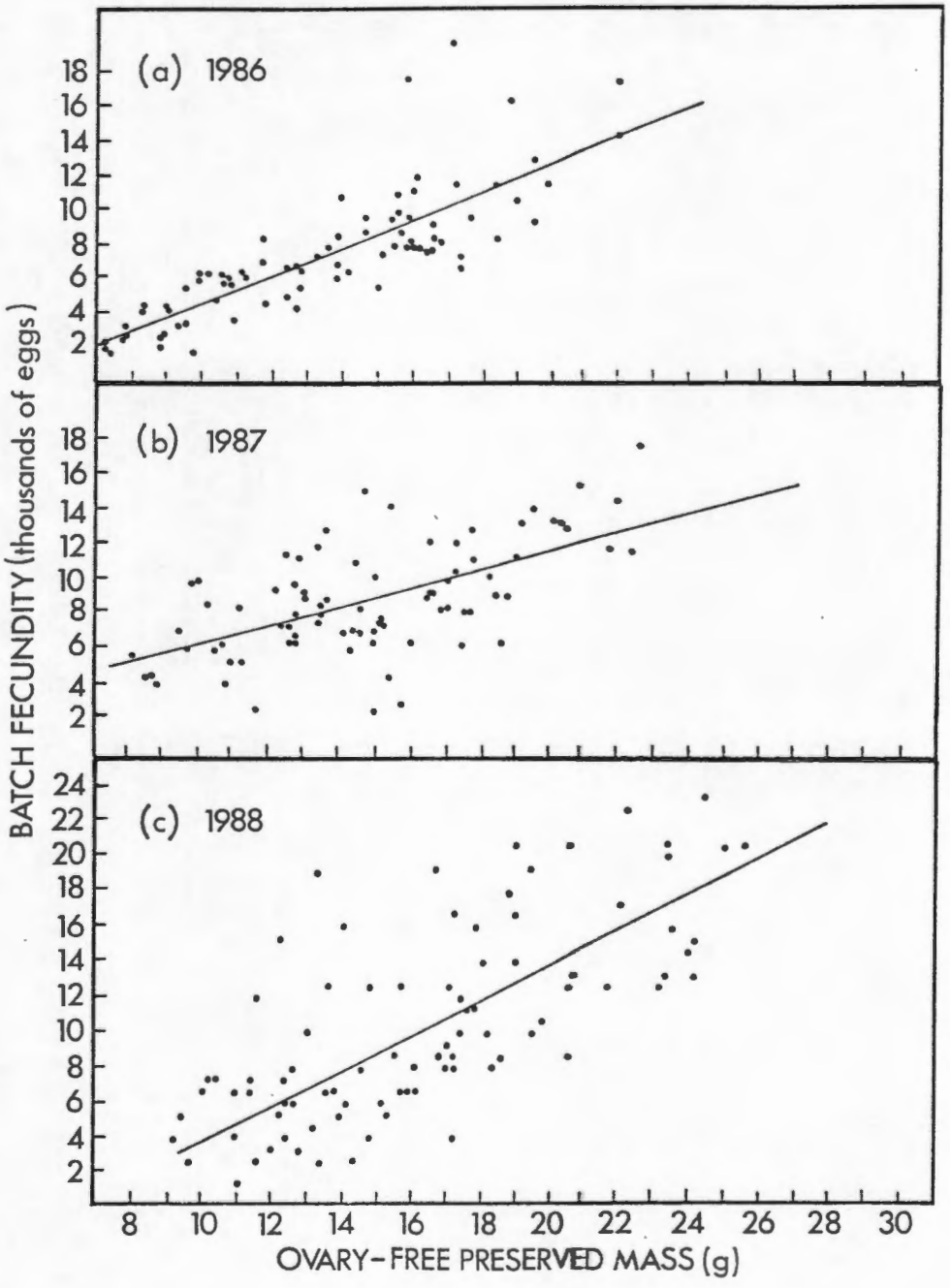


Table II: Estimated parameters of regressions of batch fecundity against ovary-free preserved fish mass (F = aW + b) plus coefficient of correlations (r), mean batch fecundity (F), mean gonadosomatic index (GSI) plus standard deviation (S.D.), mean relative fecundity (RF) plus standard deviation (S.D.), mean ovary-free preserved mass (W) of females used to calculate the batch fecundity regression parameters and number of samples (N).

	Year		
	1986	1987	1988
a	782.79	521.64	959.09
b	-3332.90	844.35	-5401.49
r	0.81	0.61	0.77
F	5627	6490	5878
GSI	12.4	14.8	16.0
SD	3.3	4.6	5.6
RF	542	582	614
SD	281	177	239
W	13.68	15.13	16.74
N	81	81	102

Gonadosomatic index (GSI) increased between 1986 and 1988 (Table II) and, also with the increases in the ovary-free weight of females (Table III). Data for individual length classes in each year are shown in Table III. Older (larger) females have a higher mean batch fecundity than younger (smaller) ones (Table III). Also, relative fecundity tends to increase with size of fish.

There were no significant differences ($P>0.7$) in the relative fecundity of fish caught in the three areas examined in 1986 (Table IV). However, in 1987 the relative fecundities of anchovy females caught on the south-west and south-east coasts were significantly different ($P<0.001$). During 1988 there was no significant difference in the relative fecundity of fish caught off the south-west and south-east coasts ($P>0.1$). Therefore, taking the three years together, no overall systematic trend of regional differences in fecundity could be noted.

IV. DISCUSSION

The trend of increasing GSI from 1986 to 1988 might have been caused by the similarly increasing trend in mean fecundity, as ovary-free weight (and thus length) of females increased (Table III). Similar trends have been reported by De Silva (1973) for sprat (*Sprattus sprattus*) off the west coast of Scotland. Also, relative fecundity was found to increase with size of fish, as also reported by Alheit and Alegre (1986). Since the average

Table III: Mean batch fecundity, mean relative fecundity and mean GSI plus standard deviations (S.D.) per weight and size classes of anchovy for three years. Length at mass was estimated according to Robinson (1966).

SAMPLE SIZE (NUMBER OF FEMALES)	CAUDAL LENGTH (cm)	MEAN OVARY-FREE PRESERVED MASS (g)	MEAN BATCH FECUNDITY (NUMBER OF OOCYTES PER FEMALE)	S.D.	MEAN RELATIVE FECUNDITY (OOCYTES PER GRAM FEMALE)	S.D.	MEAN GSI	S.D.
			1986					
6	9.0	7.52	2 299	± 536	304	± 62	7.2	± 1.3
10	9.5	9.03	5 267	± 5 934	591	± 675	8.9	± 2.6
10	10.0	10.55	5 763	± 1 654	558	± 194	11.3	± 2.4
7	10.5	11.80	5 823	± 1 479	498	± 137	12.2	± 3.3
8	11.0	13.22	6 671	± 756	505	± 56	12.5	± 1.7
14	11.5	15.27	7 898	± 2 199	517	± 147	14.0	± 2.2
17	12.0	16.78	10 140	± 3 631	606	± 218	14.3	± 2.7
7	12.5	19.44	11 474	± 2 677	591	± 141	15.6	± 1.4
2	13.0	22.58	15 937	± 2 229	706	± 97	17.2	± 3.0
			1987					
4	9.5	8.55	4 591	± 834	540	± 120	12.9	± 3.1
6	10.0	10.26	6 244	± 1 963	616	± 217	13.9	± 5.6
7	10.5	11.17	6 692	± 2 459	612	± 256	15.8	± 6.9
17	11.0	13.26	8 050	± 2 049	614	± 170	14.7	± 4.8
17	11.5	15.08	8 045	± 3 016	540	± 216	13.6	± 4.5
15	12.0	17.44	9 420	± 2 352	547	± 167	15.0	± 4.2
7	12.5	19.11	11 457	± 2 155	599	± 108	14.6	± 2.4
6	13.0	21.62	12 968	± 1 435	602	± 83	17.1	± 2.6
2	13.5	23.00	16 219	± 2 529	704	± 95	22.7	± 2.1
			1988					
3	9.5	9.36	3 927	± 1 335	421	± 148	2.0	± 3 0
6	10.0	10.44	5 856	± 1 415	564	± 146	14.2	± 2.9
14	10.5	11.94	5 800	± 2 303	490	± 206	12.5	± 3.4
14	11.0	13.52	6 984	± 3 150	526	± 266	13.4	± 5.3
12	11.5	15.14	8 364	± 4 207	567	± 314	13.7	± 4.6
18	1[illegible].0	17.09	10 416	± 3 617	610	± 214	15.4	± 2.4
11	5	19.01	12 335	± 3 477	652	± 193	17.7	± 4.9
9	13.0	21.24	16 240	± 3 366	774	± 200	19.8	± 5.9
8	13.5	23.76	17 580	± 4 469	745	± 214	20.8	± 4.9
6	14.0	25.38	21 899	± 1 655	863	± 65	26.1	± 3.6
1	14.5	28.46	19 280	±	677	±	18.0	±

Table IV: Mean relative fecundity and mean GSI plus standard deviations (S.D.) and number of samples (N) per area for the three years (areas are delimited as specified in the text).

YEAR	MEAN RELATIVE FECUNDITY (OOCYTES PER GRAM FEMALE)	S.D.	MEAN OVARY-FREE PRESERVED MASS (g)	S.D.	N	AREAS
1986	509	373	14.20	1.91	5	West Coast
	533	99	14.00	2.86	47	South-West Coast
	572	431	13.07	5.30	29	South-East Coast
1987	645	135	12.73	0.44	3	West Coast
	667	187	11.56	2.08	27	South-West Coast
	534	157	17.19	2.85	51	South-East Coast
1988	493	178	16.32	2.99	47	West Coast
	671	258	12.96	2.53	31	South-West Coast
	776	196	22.45	3.87	24	South-East Coast

weight of females used to calculate batch fecundity increased from 1986-1988 (Table II), and this was parallelled by a significant increase from 1986 to 1988 in the proportion of hydrated ovary weight to female weight ($P<0.0001$), but not followed by a significant increase in relative fecundity, it follows that ovary weight might have increased not only because of a greater number of eggs in larger fish, but because the eggs in those fish are of a larger size. Nevertheless, because the GSI of hydrated females depends, among other things, on how long before spawning the females are caught, the trend might be erroneous.

Alheit *et. al.* (1983) observed latitudinal variation in batch fecundity of the Peruvian anchovy studying a data set from 1981 and concluded that anchovies of higher latitudes might have a higher batch fecundity. The same findings were reported for the northern anchovy (Laroche and Richardson, 1980). However, a new data set gained in 1985 did not supported the hypothesis of latitudinal variation, because by dividing the data into female weight classes revealed that some of the latitudinal variation was due to relative fecundity being dependent on female weight, however, most of the variation cannot be explained in this way (Alheit and Alegre, 1986).

For the Cape anchovy, the mean ovary-free preserved mass of females per area (Table IV) revealed that some of the regional variations observed in the three years were due to relative fecundity being

dependent on female weight, however, as has been noted by Alheit and Alegre (1986) not all variations could be explained in this way.

Hunter *et al.* (1985) concluded for the northern anchovy that batch fecundity data have potentially high interannual variability. In addition, Alheit (1988) and Heidrich (1925), have concluded for sprat that batch fecundity is also highly variable intra-seasonally. In view of these reported variations, the similarity of the interannual population mean batch fecundity and relative fecundity values for the Cape anchovy between 1986 and 1988 are somewhat surprising. Similarly low interannual variation was noted by Alheit and Alegre (1986) for the Peruvian anchovy and by Alheit (1989) for the northern anchovy.

Alheit *et. al.* (1983) speculated that the causes of variability might be the food availability, because during the "El Nino" year 1976 when feeding conditions were unfavourable for the Peruvian anchovy, adults did spawn very low number of eggs. If it were the case, mechanisms such as egg cannibalism may provide enough food to compensate for potential changes in fecundity. Therefore, compensation to stock size might efficiently operates after egg production in the egg stage (Chapters 2, 4 and 5).

In 1986 the spawning biomass of the Cape anchovy was estimated by acoustics to be 1.7 million tons (Armstrong et al. 1988). In 1987,

this declined to 1.5 million tons and, in 1988, to 1.1 million tons (SFRI, unpublished data). Preliminary results for 1989 indicate an even lower stock estimate of 0.5 million tons. Although acoustic estimates have high variance, there thus appears to be a trend of decreasing biomass over the study period. Furthermore, anchovy egg data obtained yearly from 1983 during research cruises organized to estimate the spawning stock size at peak spawning show a similar decreasing trend from 1986 to 1988 (Chapter 2). Such results are consistent with acoustic estimates, bearing in mind that fecundity per female has not changed in that period. Since both the average relative fecundity and the batch fecundity stayed about the same between 1986 and 1988, there is no indication of a compensatory mechanism between batch fecundity and stock size, as has been indicated for the South African pilchard (*Sardinops ocellatus*) by Shelton and Armstrong (1983).

However, one must remember that total annual fecundity is the product of batch fecundity and the number of spawnings per year. Spawning fraction was estimated only during peak spawning. That does not give us information on the number of spawnings per year. Fecundity compensation would be possible if the number of spawnings per year changed. A further complication is that variation in egg size might be another compensatory mechanism as increases in batch fecundity may be accompanied by a decline in egg size (Alheit, 1988). Smaller eggs may decrease chances of survival as they would have less reserves and if they survive, the hatching

larvae will not be as well fed as the larva from larger eggs and will thus be more exposed to disease and predation. Batch-spawning fish therefore might have a rather complicated system by which they could regulate their annual egg output in response to variations in population density.

The results indicate that the spawning rate of anchovy females off South Africa (approximately every twelve days) is somewhat lower than that for northern anchovy which, on average, spawn every eight days (Bindman, 1986), or for Peruvian anchovy which spawn approximately once every six days (Alheit *et al.* 1983; Alheit *et al.* 1984). This difference could be attributed to the fact that the number of times a female spawns depends on the amount of energy allocated to reproduction, which in turn is dependent on the prevailing physical and biological conditions. Therefore, the lower spawning frequency in the Benguela could be indicative of lower food availability.

Hunter and Leong (1981) showed that about 65% of the annual caloric cost of spawning is supplied by fat reserves, and additional requirements for continued spawning would have to come from food assimilated and available for reproductive process over a period of only eight days for *E. mordax*, or two days for the Hawaiian anchovy *Encrasicholina purpurea* (Clarke, 1987). Egg production and reproductive effort also probably changes in a complex manner in relation to temperature. It is probable that Cape anchovy produce

larger eggs when water temperatures are cooler (Ware, 1975) since larger eggs are advantageous as water temperatures decline, because incubation periods are longer (Valdes *et. al.* 1987).

Egg cannibalism may be an important factor providing energy to continue spawning at times when alternative food is scarce (Chapter 4) and, also regulating the effective egg production as intensity of cannibalism could change with population density. Different spawning fractions in the Benguela, California or Peru may also be explained in terms of different rates of cannibalism on anchovy eggs. Ingestion of eggs by Cape anchovies could account for an average of 70 % of the total egg mortality (Valdes *et al.* 1987), while this mechanism may account for between 20 and 28 % of the total egg mortality of Californian anchovy eggs (Hunter and Kimbrell, 1980 and MacCall, 1981) and off Peru, Alheit (1987) attributed about 22 % of the total egg mortality to cannibalism. Therefore, the high incidence of egg cannibalism in the Benguela may also be indicative of lower food availability, resulting in a lower spawning fraction.

In summary, there seems to be no interannual trend in batch or relative fecundity over the period 1986 to 1988. Since according to acoustic estimates and egg data the anchovy spawning biomass decreased over the same period, no compensatory fecundity mechanism could be identified. It appears to be an upward response in the gonadosomatic index, which could be dubious because the GSI of

hydrated females depends on, among other things, how long before spawning the females were caught. However, it is also possible that changes in egg size could be operating as a compensatory mechanism. A more detailed examination of hydrated oocytes in future fecundity studies is needed to evaluate whether or not the size of oocytes is playing a role as a compensatory mechanism of changes in the anchovy spawning stock.

Although compensation could not be detected, the insight into reproductive processes of anchovy have important direct implications for fisheries managemenent, apart from its usage in the "Egg Production Method" to estimate the spawning stock size or in egg abundance data used as an index of population biomass. Current fisheries population theory claims that by fishing away the large, old fish, production is enhanced by compensatory mechanisms such as increase of growth rates, earlier maturity, and increase in fecundity. Since fecundity is strongly age dependent (Parrish et al. 1986), the reduction in age composition caused by heavy exploitation or selective harvest will greatly reduce the average fecundity per unit of biomass and result in a reduction in the length of the spawning season. Such changes would increase the danger of recruitment failure as noted by Alheit (1989).

ACKNOWLEDGEMENTS

I acknowledge my colleagues: Dr. M. Armstrong, Dr. R. Crawford, Dr. K. Cochrane, Mr. I. Hampton and Dr. Roy Melville-Smith (SFRI); Dr. M. Bergh (University of Cape Town-UCT), Professor G. Polis (Vanderbilt University, Tenneesse), Dr. C. Brownell (The Oceanic Institute, Hawaii), Dr. J. Alheit (Polarmar, Bremerhaven) and my supervisor Professor C. Griffiths (UCT) for critically reviewing earlier versions of this manuscript. All the participants of the research cruises in the R.S. *Africana* are greatfully acwnowledged for assistance in data collection. The reprographic section of SFRI is acknowledged for the artwork. This work is being submitted in partial fulfilment of the requirements of Ph.D. at the University of Cape Town.

REFERENCES

ALHEIT, J. 1986 - A new method for determining batch fecundity of hake (Genus: *Merluccius*). *ICES CM* 1986/*G*:62: 9 pp.

ALHEIT, J. 1987 - Egg cannibalism versus egg predation: their significance in anchovies. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds.). *S. Afr. J. mar. Sci.* 5: 467-470.

ALHEIT, J. 1988 - Reproductive biology of sprat (*Sprattus sprattus*): factors determining annual egg production. *J. Cons. perm. int. Explor. Mer* 44: 162-168.

ALHEIT, J. 1989 - Comparative spawning biology of anchovies, sardines, and sprats. *Rapp. P-v. Reun. Cons. int. Explor. Mer*. 191: 7-14.

ALHEIT, J. and B. ALEGRE 1986 - Fecundity of Peruvian anchovy, *Engraulis ringens*. *Working Document ICES* CM 1986/H:60: 12 pp.

ALHEIT, J., ALEGRE, B., ALARCON, V.H. and B. MACEWICZ 1983 - Batch fecundity and spawning frequency of various anchovy (Genus: *Engraulis*) populations from upwelling areas and their use for spawning biomass estimates. *F.A.O. Fish. Rep.*, 291:

977-985.

ALHEIT, J., ALARCON, V.H. and B. MACEWICZ 1984 - Spawning frequency and sex ratio in the Peruvian anchovy, *Engraulis ringens*. *Rep. Calif. coop. oceanic Fish. Invest.* **24**: 43-52.

ARMSTRONG, M.J., SHELTON, P.A.] HAMPTON, I., JOLLY, G. and Y.C. MELO 1988 - Egg production estimates of anchovy biomass in the southern Benguela system. *Rep. Calif. coop. oceanic Fish. Invest.* **29**: 137-157.

BINDMAN, A.G. 1986 - The 1985 spawning biomass of the northern anchovy. *Rep. Calif. Coop. Oceanic Fish. Invest.* **27**: 16-24.

CLARKE, T.A. 1987 - Fecundity and spawning frequency of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. *Fishery Bull., Wash.* **85**(1): 127-138.

CRAWFORD, R.J.M., SHELTON, P.A. and L. HUTCHINGS 1983 - Aspects of variability of some neritic stocks in the southern Benguela system. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose, Costa Rica, April 1983.* Sharp, G.D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(2): 407-448.

DE SILVA, S.S. 1973 - Aspects of the reproductive biology of the

sprat, *Sprattus sprattus* (L.) in inshore waters of the west coast of Scotland. *J. Fish. Biol.* 5: 689-705.

HEIDRICH, H. 1925 - Uber die fort pflanzung von Clupea sprattus in der Kieler Bucht. Wiss. Meeresunters., Neve Folge, Abt. Kiel. 20: 1-42.

HUNTER, J.R. and S.R. GOLDBERG 1980 - Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax. Fishery Bull., Wash.* 77(3): 641-652.

HUNTER, J.R. and R.J.H. LEONG 1981 - The spawning energetics of female northern anchovy, *Engraulis mordax. Fishery Bull., Wash.* 79(2): 215-230.

HUNTER, J.R. and C.A. KIMBRELL 1980 - Egg cannibalism in the northern anchovy, *Engraulis mordax. Fishery Bull., Wash.* 78(3): 811-816.

HUNTER, J.R., LO, N.C.H. and R.J.H. LEONG 1985 - Batch fecundity in multiple spawning fishes. In *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, Engraulis mordax.* Lasker, R. (Ed.). *Tech. Rep. NOAA* NMFS 36: 67-77.

LAROCHE, J.L. and S.L. RICHARDSON 1980 - Reproduction of northern

anchovy, *Engraulis mordax*, off Oregon and Washington. *Fishery Bull., Wash.* **78**: 603-618.

MacCALL, A.D. 1981 - The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis*. In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, 1980*. Sharp, G.D. (Conv. Ed.). Paris; Unesco: 201-220 (*I.O.C. Workshop Rep.* 28).

NELLEN, W. 1986 - A hypothesis on the fecundity of bony fish. *Meeresforschung* **31**: 75-89.

PARRISH, R.H., MALLICOATE, D.L. and R.A. KLINGBEIL 1986 - Age dependent fecundity, number of spawnings per year, sex ratio, and maturation stages in northern anchovy, *Engraulis mordax*. *Fishery Bull., Wash.* **84**(3): 503-517.

ROBINSON, G.A. 1966 - A preliminary report on certain aspects of the biology of the South African anchovy, *Engraulis capensis* (Gilchrist). M.Sc. thesis, University of Stellenbosch: [iii] + 61 pp. + 66 Tables.

SHELTON, P.A. and M.J. ARMSTRONG 1983 - Variations in parent stock and recruitment of pilchard and anchovy populations in the

southern Benguela system. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose*, Costa Rica, April 1983. Sharp, G.D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(3): 1113-1132.

VALDES, E.S., SHELTON, P.A., ARMSTRONG, M.J. and J.G. FIELD 1987 - Cannibalism in South African anchovy: egg mortality and egg consumption rates. In The Benguela and Comparable Ecosystems. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 613-622.

WARE, D.M. 1975 - Relation between egg size, growth, and natural mortality of larval fish. *J. Fish. Res. Bd Can.* **32**: 2503-2515.

C H A P T E R 2

ABUNDANCE OF CLUPEOID EGGS IN THE BENGUELA ECOSYSTEM AND RECRUITMENT OF ANCHOVY *Engraulis capensis*

Edy S. Valdes
Sea Fisheries Research Institute, Private Bag X2, 8012 Rogge Bay, South Africa

Key words: *Engraulis capensis*, *Sardinops ocellatus*, egg abundance, anchovy recruitment, South Africa.

ABSTRACT

The abundance of eggs of anchovy *Engraulis capensis* and sardine *Sardinops ocellatus*, is used as the basis of a model aimed at estimating anchovy recruitment. The model's hypothesis is based on the existence at the egg stage of compensatory mechanisms, which potentially may contribute largely to mortality. These mechanisms are cannibalism of adult anchovy on their own eggs and predation by sardine on the same eggs, and they are considered to be the most important factors affecting survival to recruitment in the anchovy. The implication of different concentrations of eggs and different co-occurence levels of the two species are discussed in the light of cannibalism and intraguild predation and their effects on anchovy recruitment. In general, the output of the model for several concentration levels and overlapping indices shows that the anchovy population appears as a saturated population when the index of overlapping is constant and is highly concentrated, or when

predators are highly concentrated, producing poor recruitments. According to the model, a decrease in concentration indices for anchovy and sardine and a decrease of the overlapping index may lead to either a decrease or an increase in the abundance of eggs, depending on the sardine biomass and hence on the relative importance of intraguild predation and intraspecific predation on anchovy eggs at the time. The existence of an interaction between guild species potentially determines anchovy recruitment and should thus be used to establish a joint management scheme for guild species.

I. INTRODUCTION

Fisheries for anchovy and sardine are known to vary markedly from year to year, often with severe socio-economic consequences (Glantz, 1984; Glantz *et al.* 1987). Fishery management cannot yet forecast these variations, largely because the causes of recruitment variability remain unpredictable and in most cases unknown.

While fishing is one source of mortality of fish, scientists who have studied the fluctuations of fish populations have not yet been able to reach any definitive conclusion as to whether it has been the source of any clupeoid collapse. Clark and Marr (1955) had opposing views regarding the collapse of the Pacific sardine. Clark felt that each year-class was related to stock size and that it was density-dependent. Marr, on the other hand, argued that weak

year-classes were caused by adverse environmental factors and that these had caused the sardine's disappearance (density-independent). Soutar and Isaacs (1969, 1974) reported the results of palaeoecological investigation of fish scales in sediments and showed that declines and increases of both Pacific sardine and northern anchovy species had taken place even before the fisheries were established.

Among the greatest of Hjort's (1914) enduring contributions to understanding the population dynamics of marine fish was his recognition that fluctuations in catches of commercially important species were due to changes in population abundance and not simply to migrations of the species across large areas. He recognized that changes in abundance resulted largely from variable survival of new year-classes before they were recruited to the fishery. He proposed that larval transport away from favourable nursery areas and mass starvation of larvae at the time of first feeding, were potential causes of the extreme variations in year-class strength.

Recent theories have elaborated on Hjort's ideas of feeding conditions and focused on the distribution of larval food in the water column (Lasker 1975) or the match-mismatch of spawning by fish and production of larval food (Cushing 1972, 1975). Transport mechanisms, oceanographic retention mechanisms, and the timing of spawning have also been implicated as being important causes of variations (Parrish *et al.* 1981; Sinclair and Tremblay,

1984). Other theories have suggested the importance of variability in the environment, a subject not clearly understood (Koslow, 1984; Shepherd *et al.* 1984) to species dominance interactions (Skud, 1982).

Walters (1984) proposed that, because climatic factors are largely unpredictable, a probability distribution would likely be more useful than a single prediction of recruitment. However, in spite of this proposal, considerable research effort is still being channeled into the cause of recruitment variability in fish (Bakun *et al.* 1982) with the objective of determining the underlying density-dependent population response.

Bakun (1985) presented a useful summary of hypothethical controls on survival of the early life stages of fish. These he listed as starvation, predation, advection, physiological stress and disease. Hjort's theories and recent attempts to develop a unifying theory for recruitment variation have, however, not considered predation to be important. Nevertheless, some investigators (e.g. Ware, 1975; Shepherd and Cushing, 1980; Sissenwine, 1984) have conceived conceptual models which propose predation to be a key factor in recruitment. Also, Hunter (1981, 1984) stressed that predation is probably the main cause of mortality in many species. In the Peruvian ecosystem, predation by *Sardinops sagax* on anchovy eggs had been reported as an important source of mortality for anchovy eggs. It has been considered as having a greater effect on egg

mortality than anchovy egg cannibalism itself and potentially effecting the anchovy recruitment (Santander *et al.* 1983; Alheit, 1987). Butler and Pickett (1988) discussed predation by adult northern anchovy *Engraulis mordax* on *Sardinops sagax* larvae and its implication in recruitment variability.

Predation (including cannibalism), is especially important from a manager's perspective because it is often proposed as a cause of density-dependent regulation in stock-recruit relationships (Ricker, 1954; Csirke, 1980; MacCall, 1981; Rothschild, 1986). Predation as an underlying density-dependent population response in fish populations is obscured by the environmentally caused variability and by error in the measurement of both recruitment and spawner stock size (MacCall, 1980). Therefore, prediction of recruitment on the basis of spawner stock size alone is unlikely to be very useful in the context of clupeoid management. A comparison of the temporal and spatial patterning of environmental variability with the life history characteristics of the species may, on the other hand, be very important. Multispecies interactions which focus on predator-prey relationships are generating increasing interest, especially when fishing pressure on one species may influence the abundance of another (Merce, 1982; Gulland and Garcia, 1984).

Catches of clupeoids have fluctuated in several ecosystems and it has been assumed they represent fluctuations in the stock sizes.

Stocks of Californian sardine *Sardinops caerulea*, Peruvian sardine *S. sagax* and Far Eastern sardine *S. melanostictus* as well as the South African pilchard (for convenience hereafter called sardine) *Sardinops ocellatus* have collapsed and been followed by apparent increases in the size of anchovy stocks (Kawasaki, 1983). Shannon *et al.* (1988) reported increases in the anchovy catch (*Engraulis capensis*) in the southern Benguela ecosystem in the late 1959's, in the early 1970's and again recently (1987). These increases have followed collapses or severe depletions in the stocks of the cohabiting South African sardine. During the 1950s and 1960s, sardine dominated purse-seine catches in the South-East Atlantic (Crawford *et al.* 1990), and after their collapse in the southern Benguela, they were largely replaced in purse-seine catches by anchovy, a species which, like the sardine, seems to thrive particularly in warm conditions (Shannon *et al.* 1988).

The effect of anomalies in sea surface temperature on clupeoids indicates that moderate advection of warm water may be advantageous, whereas exceptional warming may cause diminished reproductive success (Shelton *et. al.* 1985). In the Benguela region, spawning of sardine and anchovy is associated with the mixing areas between Benguela Current water and warm surface water advected into the system from the Agulhas Current (Crawford *et al.* 1983). Sites of strong offshore transport are avoided by spawners, even though productivity may be highest in these areas. Rapid development of eggs in the warmer water may result in increased survival of

larvae, and first-feeding larvae may also benefit from the concentrations of food associated with the strong fronts and thermoclines set up by the interplay between upwelling, advective processes and solar heating.

Estimates of secondary production across the anchovy spawning habitat (Peterson and Hutchings, 1989) have shown that production rates of copepod eggs over the offshore part of the western Agulhas Bank tend to be low because the thermoclines are deep, the rate of primary production is low and the size-spectra and/or species compositions of the phytoplankton are suboptimal for copepod feeding. In a given area, the food consumed by fish will be a function of the density of clupeoids, the relative concentrations of different food particles as perceived by the fish and the overall concentration and size distribution of food items which determine the mode of feeding (filtering or biting) in those species that can alternate between the two modes. Food consumption by the fish in turn modifies the biomass and size composition of the plankton.

As most anchovy spawning takes place in the western Agulhas Bank, there is potential for anchovy and sardine to deplete plankton standing stocks to a level at which a large fraction of anchovy egg production could be consumed by the fish. Variations in the temperature structure over the spawning habitat, which could result in concentration or expansion of the area covered by the stock, are

likely to have a synergistic effect, because the fish would be less or more exposed to density-dependent population responses such as anchovy cannibalism on eggs, or sardine predation on the same eggs. Abundance-related expansion and contraction of range has been observed for other stocks of clupeoids (Murphy, 1967, 1977), and may be one of the main reasons for their susceptibility to collapse (MacCall, 1976; Lasker and MacCall, 1983).

The occurrence of water warmer than 20°C on the Agulhas Bank in late summer and early autumn appears to reduce the area suitable for spawning and concentrate adult spawning fish closer inshore (Shelton *et. al*, 1985). Very few anchovy eggs are found in this warm water probably as a result of cannibalism. At this time the catch rate of adult anchovy by the purse-seiners operating inshore increases (Shelton *et al*. 1985). If food abundance is low, the harvest may be appropriate in order to increase recruitment (MacCall, 1981). A decline in the catch rate of adult anchovy in late autumn is coincident with the seasonal cooling of surface waters on the Agulhas Bank (Shelton *et. al*. 1985). By winter the warm water is confined to the body of the Agulhas Current, and there is a marked eastward movement of anchovy and sardine in autumn (Crawford, 1981a, 1981b). Dispersal after spawning is predominantly northwards and westwards (Shelton and Hutchings, 1982), and recruits may benefit from the consistently high standing stock of plankton inshore between Lambert's Bay and Cape Town (Shelton *et al*. 1985).

The aim of this paper is to model anchovy recruitment dependence on the number of anchovy and sardine eggs. By means of a simple model of competition between anchovy and sardine Murphy (1967) demonstrated that, when the interspecific interaction coefficients were equal and population growth was not affected by environmental variability, anchovy, which were shorter lived, had a faster rate of population growth and a smaller carrying capacity, increased in biomass more rapidly and then collapsed, while the sardine population continued to grow to carrying capacity. In the following account, a model based on that of Csirke (1980) is used to obtain a recruitment index for anchovy generating Ricker's-type recruitment curves based on egg abundance, rather than fish biomass. The hypothesis is advanced that anchovy recruitment may vary as a direct result of the differential rates of cannibalism and sardine predation on anchovy eggs resulting from changes in the habitat size of both species (perhaps triggered by the environment) and the degrees of overlapping between both.

II. MATERIALS AND METHODS

1. Survey design

Surveys were carried out in November of each year between 1983 and 1988, November being generally the month of peak anchovy spawning (Armstrong *et al.* 1988). The surveys were conducted on board the Sea Fisheries Research Institute's R.S. *Africana* according to the

design described in Armstrong *et al.* (1988). The main purpose of the surveys was to estimate the spawning biomass of anchovy (Hampton, 1987). In 1983 and 1984 they were based on a systematic grid of transects running approximately perpendicular to the coastline and spaced 37 km apart at the inshore stations (Fig. 1). From 1985 to 1988 (Figs 2 and 3), the survey area was stratified according to consistent patterns of fish distribution observed in the previous spawning surveys. Within each stratum, the spacing between transects was randomized within limits to allow variances to be estimated on the assumption of random sampling. The surveys from 1985 to 1988 covered areas similar to those in the 1984 survey.

2. Collection of eggs and the estimation of egg abundance

Anchovy eggs were sampled at stations spaced 9.3 km apart by means of vertical hauls of a CalVET net (Smith *et al.* 1985) from 200 m or from just above the sea bed, whichever was shallower. In areas of zero abundance of eggs the distance between samples was frequently extended to 18.6 km.

The number of eggs per station was averaged to give transect estimates, values for any omitted stations being obtained by interpolating between those 18.6 km apart on the same transect as used by Armstrong *et al.* (1988). The mean values per stratum were then calculated as the weighted mean of the transect values,

Fig. 1: The grid used in the survey of anchovy in November 1983 and 1984.

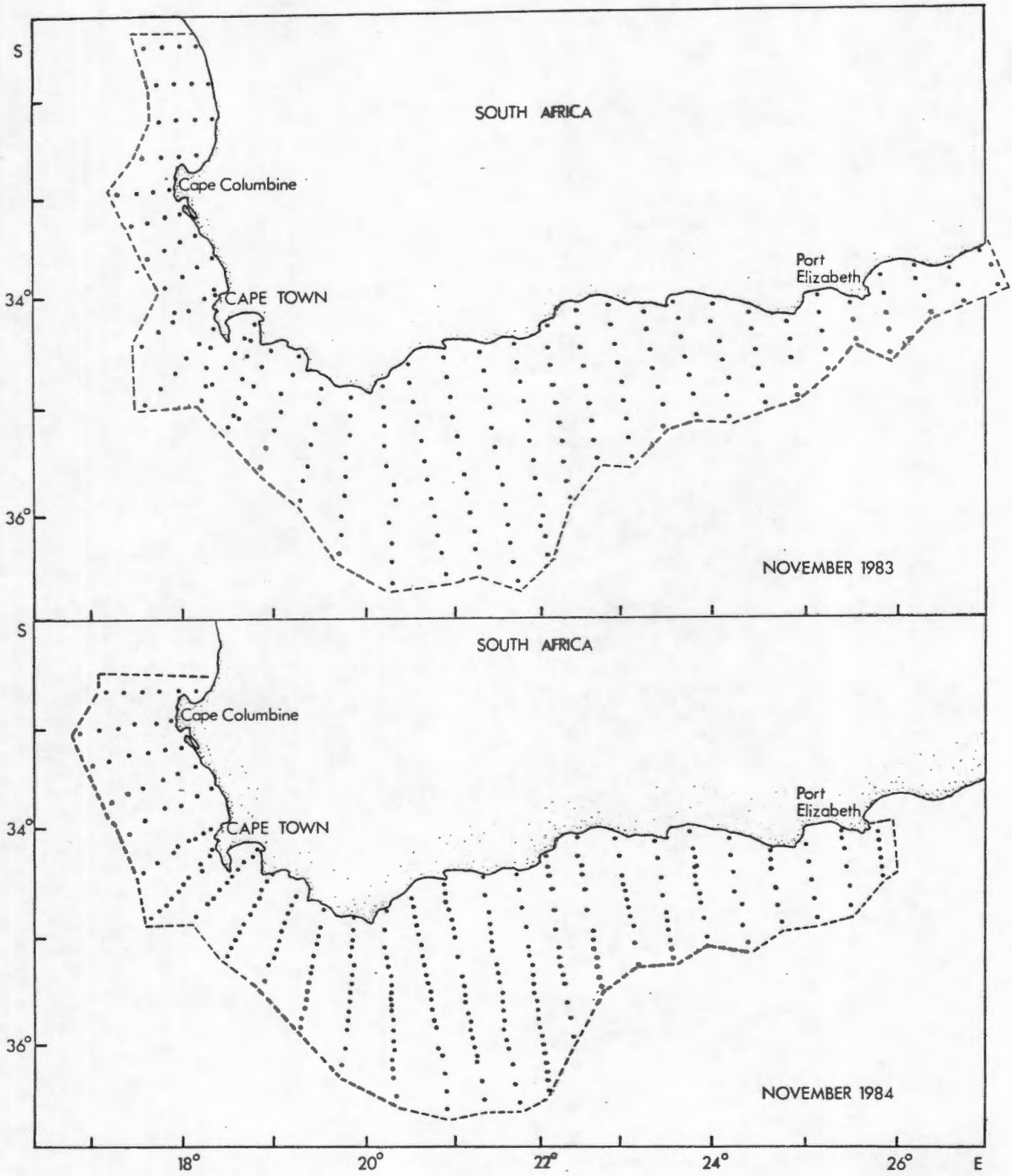


Fig. 2: The grid used in the survey of anchovy in November 1985 and 1986.

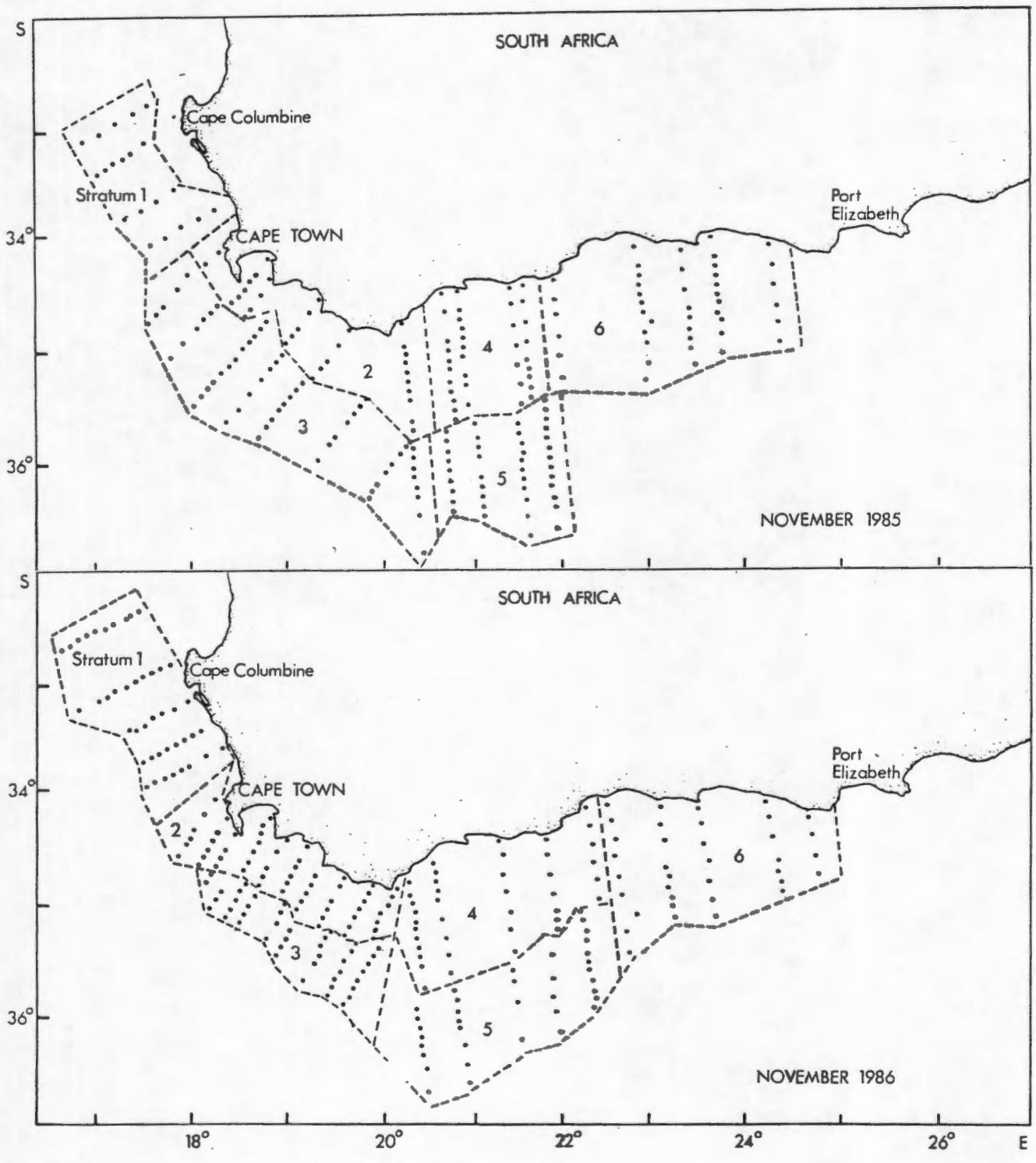
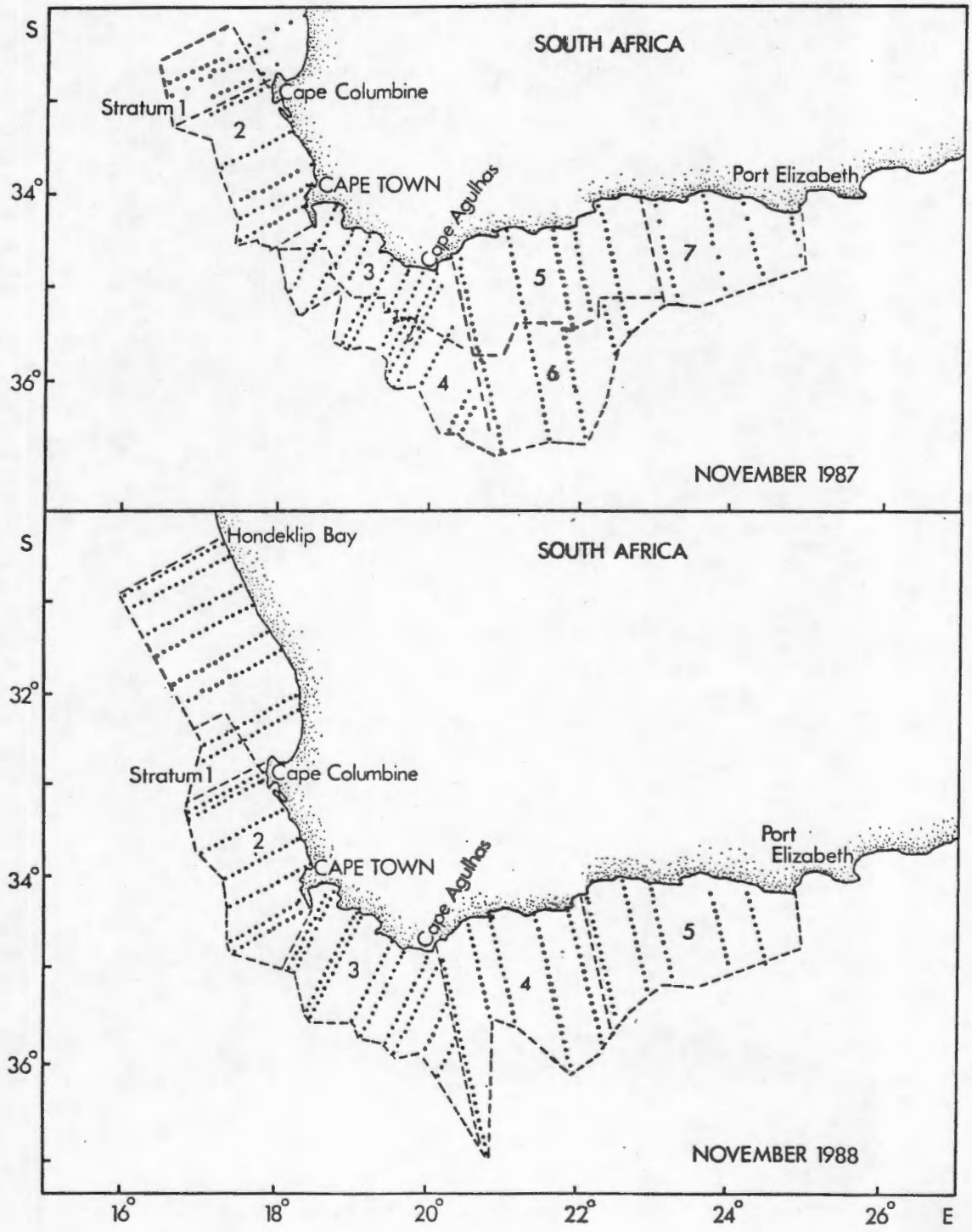


Fig. 3: The grid used in the survey of anchovy in November 1987 and 1988.



weighting being according to the length of the transects. The mean value for each survey was obtained by weighting the value calculated for each stratum by its area. The variance was obtained according to the method of Armstrong *et al.* (1988).

3. Rationale and postulation of the anchovy recruitment model

Information on the distribution and abundance of anchovy and sardine and their eggs off the West and South coasts during peak anchovy spawning has been obtained by means of acoustics (Hampton, 1987) in conjunction with midwater trawling and plankton sampling. Analyses of stomach contents gave clear evidence of the importance of anchovy egg cannibalism and predation by sardine to egg production estimates at the local scale (Valdes, 1986; Valdes *et al.* 1987).

The fraction of egg production consumed in a given area will be a function of the density of clupeoids there, as well as of the overall concentration and size distribution of food items' which will in turn determine the mode of feeding in those species which can alternate between filtering and biting. The food consumption by the fish in turn modifies the biomass and size composition of the plankton (Chapters 3 and 4).

As most anchovy spawning takes place on the western Agulhas Bank where copepod production is low, there is potential for the

different clupeoid species to deplete plankton standing stocks to a level at which a large fraction of the anchovy egg production could be consumed (Chapter 5).

Variations in the temperature structure over the spawning habitat, which could result in concentration or expansion of the area covered by the stock, are likely to have an additional strong influence on egg predation and cannibalism rates. Recent expansion of the sardine population in the southern Benguela has resulted in an increasing co-occurrence of sardine and anchovy in their spawning habitat. Therefore, interaction may lead to suppression and eventual replacement of one clupeoid species by the other as a result of density-dependent mechanisms (Chapter 5).

Because batch fecundity of anchovy was determined more or less at the same time of the spawning season in each year (Chapter 1) and was unchanged from 1986 to 1988 (Chapter 1), it was assumed that the decreasing biomass of anchovy eggs in the same period (Fig. 4) roughly reflected the decrease in the adult stock. Similar results have been obtained by acoustic data. The number of sardine eggs increased 8-fold between 1983 and 1988 (Fig. 5) and is also taken as a rough index under "normal conditions" of population increase of that species. Therefore, it is assumed that the variation in the number of eggs of the two species (Figs 4, 5) are indicative of stock fluctuations and may well be the result of interaction between the two species.

Fig. 4: Mean density of anchovy eggs S_1 and the mean fraction of positive stations with anchovy eggs FA each year, 1983-1988.

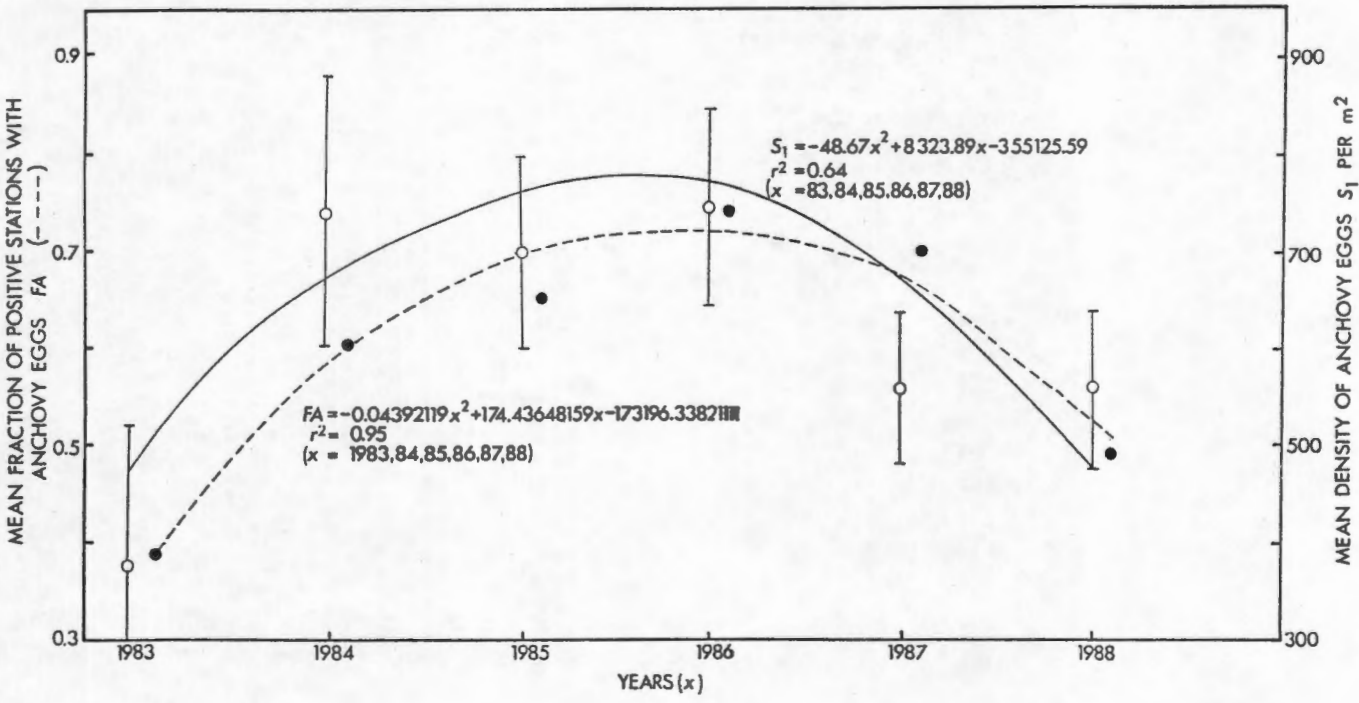
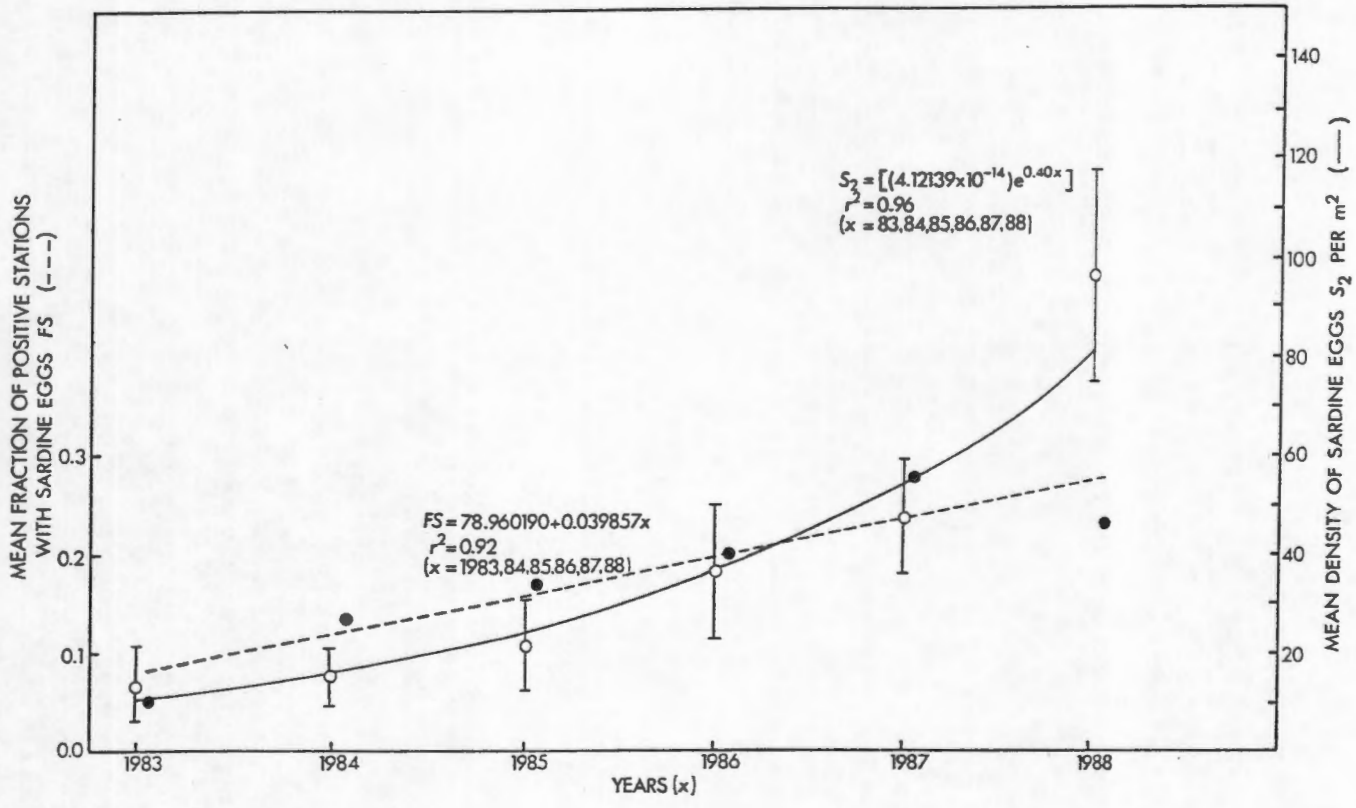


Fig. 5: Mean density of sardine eggs S_2 and the mean fraction of positive stations with sardine eggs *FS* for each year, 1983-1988.



The model used to estimate anchovy recruitment from anchovy and sardine egg numbers employed the spawner-recruit relationship proposed by Ricker (1954, 1958), which is commonly expressed as:

$$R = a\ P\ e^{(-b\ P)} \quad , \qquad (1)$$

where R is recruitment, P is the size of the spawning stock, a is a constant which includes the density-independent rate of mortality and b is a constant including the density-dependent coefficient of mortality. Based on the original interpretation Ricker (1954, 1958) gave to each parameter of his equation, where a is related to the number of eggs produced and b to the density of eggs, or the spawners and, according to Csirke (1980), the Equation (1) can be rewritten as:

$$R = a\ B\ e^{(-b'\ S)} \quad , \qquad (2)$$

where B represents the abundance (numbers) of eggs and S the density of those eggs. With this formulation, we have a three-dimensional equation which relates the number of eggs to the resultant recruitment. The density of eggs is introduced as a function of two variables: the abundance of eggs B and their dispersion or concentration. A similar relationship between adult density and biomass was postulated by Csirke (1980). This relationship can be expressed for each year i by:

$$S_i = p\ Q_i\ B_i \quad , \qquad (3)$$

where p is a constant representing the mean relationship existing under average conditions between the egg population density S and its total abundance (numbers) B. Q is an index of concentration, or dispersion, of this total biomass in relation to the expected value under average conditions (Table I).

The concentration coefficient Q would be 1.0 when average conditions exist, assuming that under such conditions the distribution pattern is normal. Otherwise, the coefficient will take values either above, or below, 1.0, depending on whether the population of eggs is more, or less, concentrated than normal. With this concept, and introducing an index of non-overlapping between anchovy and sardine and assuming that the compensatory intraspecific mortality occurs mainly when there is no co-occurrence of both species, it is possible to rearrange Equation (2) as follows:

$$R_i = a\ B_{i-1}\ e^{(-b\ B_{i-1}\ Q_{i-1}\ O_{i-1})} \qquad (4)$$

where, for each year i,

R = anchovy recruitment

B = total abundance of eggs

Q = concentration coefficient of eggs

O = index of non-overlapping between anchovy and sardine

a = a constant that includes the non-compensatory survival rate to recruitment

Table I: Estimates of concentrations of anchovy (Q_1) and sardine (Q_2) eggs during the peak spawning season (November), 1983-1988.

YEAR	Q_1	Q_2
1983	1.04	1.12
1984	1.01	1.08
1985	1.03	1.09
1986	1.19	1.27
1987	0.84	0.90
1988	0.93	1.00

b = a constant that includes the compensatory mortality coefficient

B_{t-1} refers in the model of Csirke (1980) to the spawning stock of the year previous to that in which recruitment is taking place. Here, similar nomenclature is used because reference is being made to the number of eggs in the previous year which, in general, are proportionally related to the previous year's spawner stock (an exact proportionality occurs for those years when fecundity did not change, i.e. 1986 - 1988 for anchovy in the southern Benguela). Thus, the egg data are an index of adult stock size.

To this model, using egg numbers rather than adult biomass, was added a term that included interspecific compensatory mortality according to size, concentration and the degree of overlapping between anchovy and sardine (the predators of the eggs). The degree of overlapping was considered to be 1 when there was a complete overlapping between the two species. The positive trawls for both species as a proportion of the total number of anchovy trawl catches made in the November surveys for the specified years was considered to be the index of overlapping. The proportion of negative trawls was considered to be the index for non-overlapping (Table II). With this term Equation (4) becomes:

Table II: Estimates of index of overlapping (O_2) and non-overlapping (O_1) between anchovy and sardine during November of 1984-1988.

YEAR	INDEX OF OVERLAPPING (O_2)	INDEX OF NON-OVERLAPPING (O_1)
1984	0.45	0.55
1985	0.66	0.34
1986	0.70	0.30
1987	0.66	0.34
1988	0.58	0.42

$$R_{1i} = a\ B_{1i-1}\ e^{(-b\ B_{1i-1}\ Q_{1i-1}\ O_{1i-1})}\ e^{(-c\ B_{2i-1}\ Q_{2i-1}\ O_{2i-1})} \quad (5)$$

where for each year (i):

R_1 = anchovy recruitment

B_1 = total abundance (numbers) of anchovy eggs

B_2 = total abundance (numbers) of sardine eggs

Q_1 = concentration coefficient of anchovy eggs

Q_2 = concentration coefficient of sardine eggs

O_1 = index of non-overlapping between anchovy and sardine

O_2 = index of overlapping for the two species

a = a constant that includes the non-compensatory survival rate for anchovy eggs to recruitment

b = a constant that includes the intraspecific compensatory mortality coefficient depending on the concentration and size of B_1 and on the degree of non-overlapping of both species

c = a constant that includes the interspecific compensatory mortality coefficient depending on the concentration and size of B_2 and on the degree of overlapping of both species

III. RESULTS

1. Empirical data : egg abundances

Data on the co-occurrence of anchovy and sardine eggs in November/December 1983 - 1988 provide indices of abundance of both species. Mean anchovy egg abundance and the fraction of positive stations during the surveys are reflected on Figure 4 and the same parameters for sardine on Figure 5. Data were regressed by means of a linear least squares method (SAS Institute Inc. 1982). On Figure 4 data were regressed to fit a quadratic function showing that anchovy, after a peak in 1986, suffer a clear decrease in the number of eggs and the fraction of positive stations.

In the case of sardine both number of eggs and the fraction of positive stations increased throughout the six years (Fig. 5).
The exponential curve fitted to the sardine data (Fig. 5) indicates that egg density increased faster than the number of positive stations. In other words, sardine are probably crowding their current areas of distribution before they colonize new areas.
At the present level of the resource, sardine distribution has been generally outside the area of the anchovy's distribution, therefore the co-occurence in anchovy habitat increased more slowly than the increasing rate of sardine egg abundance.

2. Results of the model

A functional regression line relating numbers (B_1) and density values of anchovy eggs (S_1 -expressed as eggs m^{-2}) for the years 1983 - 1988 is shown in Fig. 6. The equivalent regression for sardine is given in Figure 7. The respective slope coefficients p_1 (7.86708×10^{-12}) and p_2 (7.35396×10^{-12}) were then applied to estimate the concentration coefficients (Q_1 and Q_2) for the same years as: $Q_1 = S_1/(p_1 \times B_1)$ and $Q_2 = S_2/(p_2 \times B_2)$, being S_2 = density of sardine eggs.

Reducing Equation 5 to its logarithmic form and fitting it by least squares to the series for 1984-1988 (there is no recruitment value corresponding to 1983 anchovy biomass because recruitment surveys started in 1985, corresponding to 1984 spawning stock), the following parameters were estimated:

$a = 4.8 \times 10^{-8}$

$b = 4.8 \times 10^{-14}$

$c = 2.3 \times 10^{-13}$

Thus, recruitment to the southern Benguela anchovy resource can be expressed mathematically as:

$$R_{1i} = (4.8 \times 10^{-8})\ B_{1i-1}\ e^{-(4.8 \times 10^{-14})\ (B_{1i-1}\ Q_{1i-1}\ O_{1i-1})}\ e^{-(2.3 \times 10^{-13})\ (B_{2i-1}\ Q_{2i-1}\ O_{2i-1})} \quad (6)$$

Fig. 6: Relationship between the anchovy egg density S_1 and abundance B_1 (numbers) in the Benguela ecosystem during November of 1983-1988.

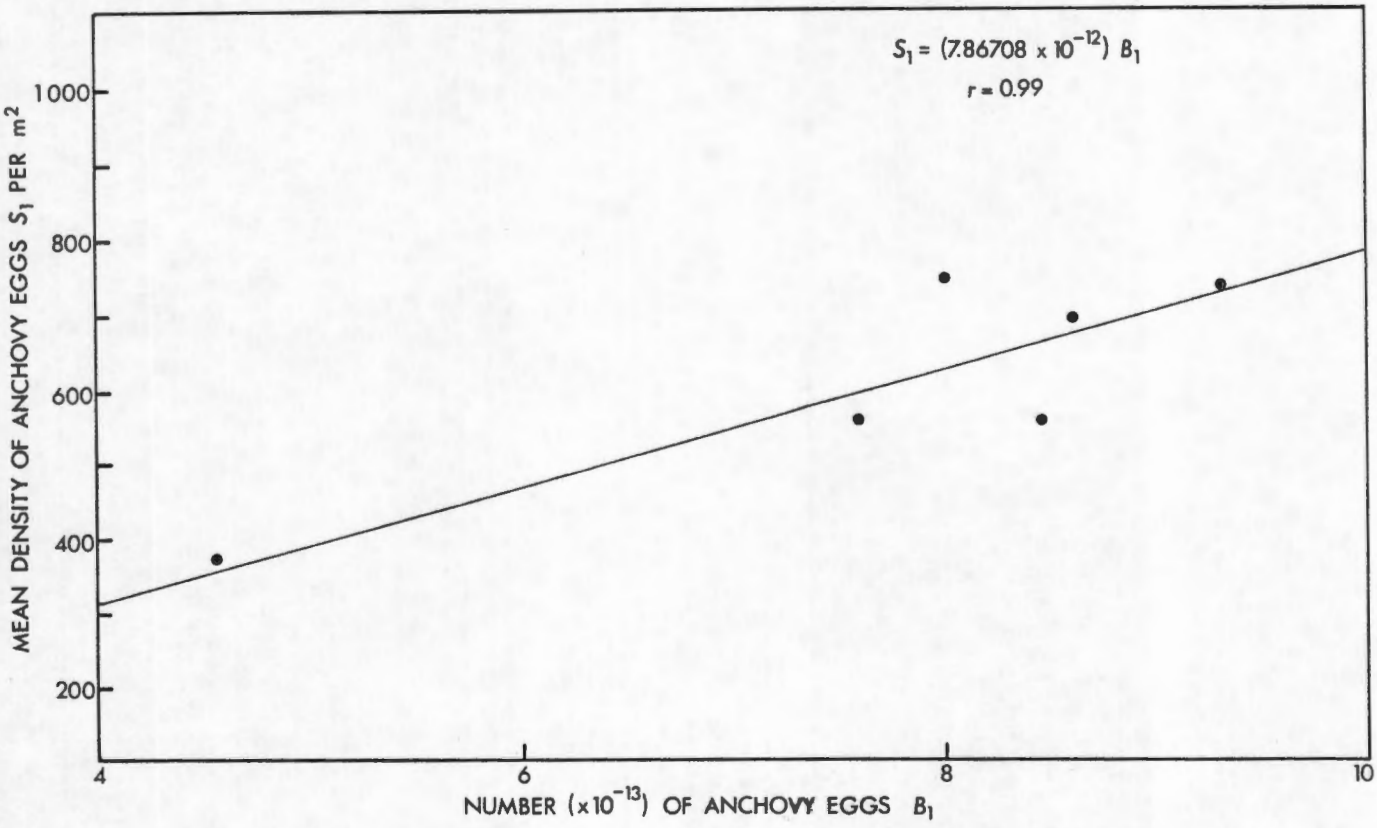


Fig. 7: Relationship between the sardine egg density S_2 and abundance B_2 (numbers) in the Benguela ecosystem during November of 1983-1988.

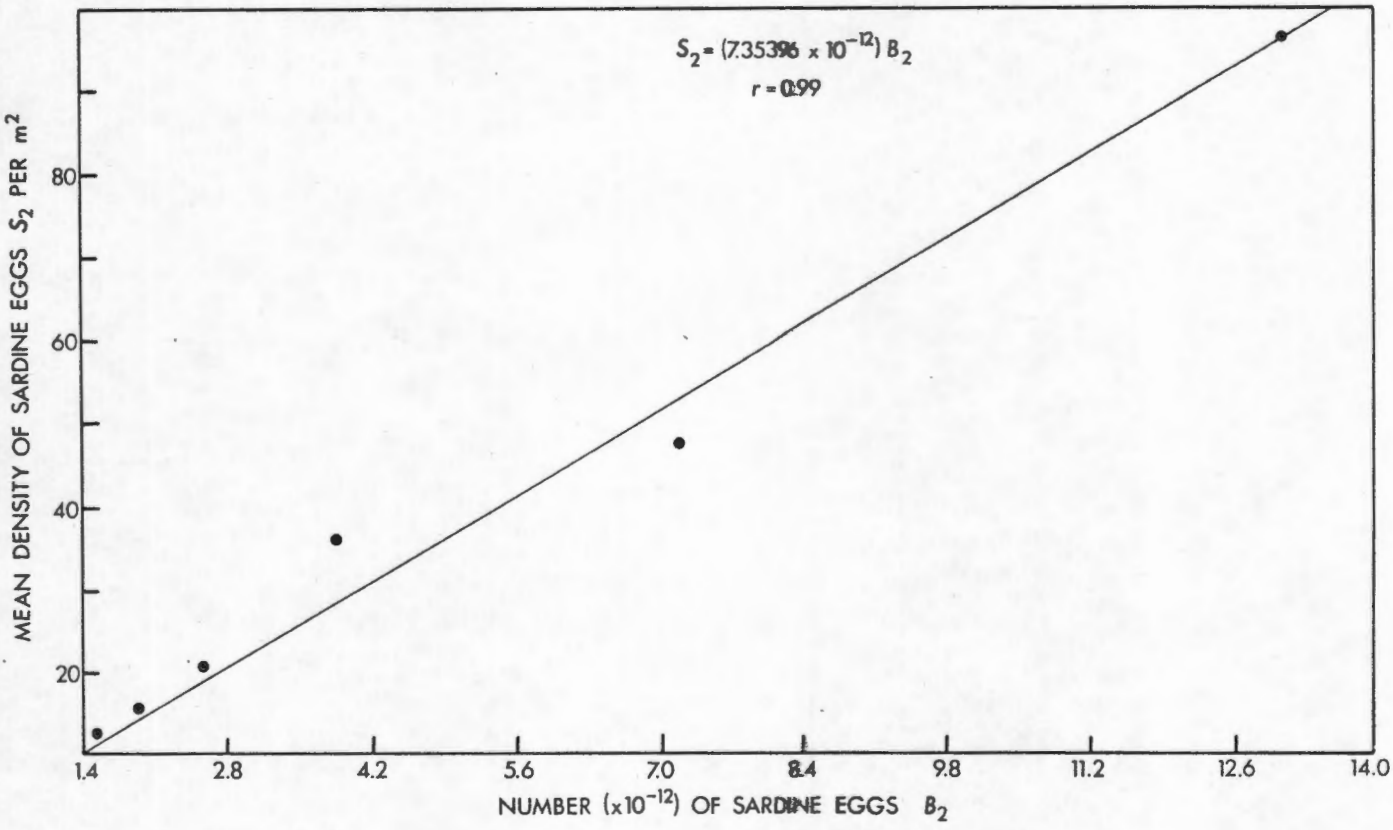


Figure 8 shows the relationship between egg abundances ($B1$, B_2), their concentrations (Q_1; Q_2); habitat overlap (O_1; O_2) and the anchovy recruitment (R_1) for several sets of arbitrary values together with a plot of the expected recruitment values (Table III) for the observed concentrations and overlapping indices for the years 1984-1988 (Tables I and II). The correspondence between expected and observed recruitment for those years is good (r = 0.81; regression coefficient = 0.83; intercept is not significantly different to 0.0, $P>0.7$).

IV. DISCUSSION

The Ricker model applied in this paper is based on the theory of a predator-prey system where the eggs or larvae are prey randomly encountered by the predator and where any increment of eggs or larvae is simultaneously followed by an increment of the predators (Ricker, 1958). Obviously, the simplest case of a compensatory mechanism of this nature would occur when parents are, at the same time, the predators of their own progeny (Csirke, 1980).

Cannibalism by the northern anchovy may be a significant source of egg mortality (Hunter and Kimbrell, 1980). These authors also made plankton tows in front of and behind a school of anchovy, and found eggs to be 48% less abundant behind the school, presumably because of cannibalism. Alheit (1987) reported that egg cannibalism accounted for 21.9% of the daily egg mortality in Peruvian anchoveta (*Engraulis ringens*), and noted that sardine (*Sardinops*

Fig. 8: Recruitment R_1 of the Cape anchovy and its dependence on egg abundance B_1, B_2 (numbers) for different set of values (i.e. series) for concentrations Q levels and overlapping O indices, 1984-1988:

Series A: Q1= 1.2; Q2= 0.9; O1= 0.1; O2= 0.9
Series B: Q1= 1.2; Q2= 1.9; O1= 0.1; O2= 0.9
Series C: Q1= 0.8; Q2= 0.9; O1= 0.4; O2= 0.6
Series D: Q1= 0.8; Q2= 1.3; O1= 0.4; O2= 0.6
Series F: Q1= 0.8; Q2= 0.9; O1= 0.8; O2= 0.2
Series G: Q1= 0.8; Q2= 1.3; O1= 0.8; O2= 0.2
Series H: Q1= 1.2; Q2= 0.9; O1= 0.8; O2= 0.2

Series E: predicted recruitment for observed values of independent variables (see Tables I and II for observed values).

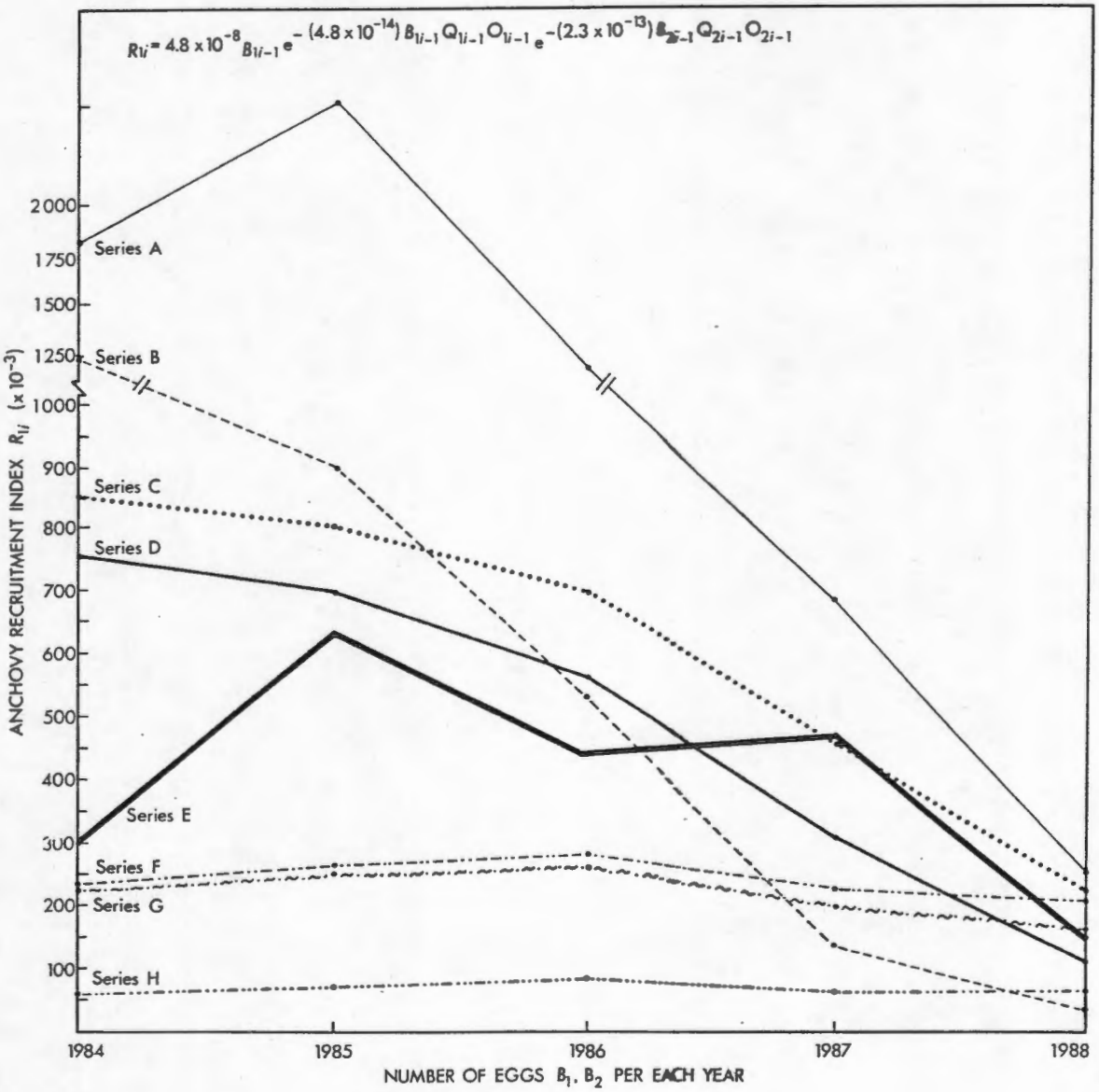


Table III: Annual estimated by the model and observed (from Armstrong *et. al.* in prep.) recruitment of the South African anchovy, 1984-1988 (thousand tons).

YEAR	RECRUITMENT	
	EXPECTED	OBSERVED
1984	297 494	310 000
1985	628 931	466 000
1986	433 887	575 000
1987	467 274	508 000
1988	146 833	132 000

sagax) were also important predators on anchoveta eggs. Such a mechanism also appears to apply in the southern Benguela anchovy population because cannibalism has been observed during 1984 and 1985 in a specific area of high egg density of the western Agulhas Bank by Valdes (1986) and Valdes *et al.* (1987). They estimated that cannibalism by adult anchovy on their eggs may have accounted for 30 - 100% of the total egg mortality, with a best estimate of 70% for a specific area of intensive spawning over the Agulhas Bank.

This cannibalistic behaviour was shown to be a potentially important density-dependent compensatory mechanism of the size of the adult stock by regulating egg survival as a function of egg density (Valdes, 1986). Cannibalism by larval anchovy 15-35 mm long on eggs and smaller larvae was found to occur in laboratory experiments and was found to be potentially important in a subsequent modelling exercise (Brownell 1985, 1987). On the basis of his results, Brownell suggested that recruitment of Cape anchovy could well be density-dependent. Anchovy cannibalism and sardine predation on early anchovy larvae has been also observed by White (1988) and he postulated that it is a sort of compensatory mortality on eggs and larvae (eggs, on average, last only up to three days before hatching). Furthermore, cannibalism on late larvae has been observed by O'Toole *et. al.* (in prep.) and they also suggested that it may be density-dependent. However, competition between the larval stages cannot be discarded as another possible cause for autoregulating mortality of young anchovy, at

least until some observations on the subject have been made.

A possible relationship between population density and abundance was considered here, where the egg population density, expressed as the number of eggs per tow (or eggs per unit area), is proportional to the total biomass if environmental conditions and areas of distribution remain constant, or if they referred to average conditions for long periods of time. An average proportionality coefficient (p, in equation 3) was computed for the period 1983-1988, but a year-to-year relationship cannot be established owing to the observed fluctuations in both environmental conditions and distribution patterns over the six years (Figs 9, 10, 11).

Fluctuations in the catch per unit effort (eggs per tow) can result from variations in the catchability coefficient q. This coefficient is inversely proportional to the area inhabited (Paloheimo and Dickie, 1964) and as Gulland (1977) and Csirke (1980) have noted, the fluctuations in the environmental conditions and the distributional area can be responsible for fluctuations in the catchability coefficient. Since there are no variations due to possible changes in the sampling strategy for eggs, and because eggs are incapable of independent movement (there is no possibility of avoiding the net), our computed concentration coefficient Q is related to the catchability coefficient q, and its fluctuations can be interpreted as being representative of the size of the total area, or of the total volume inhabited by each

Fig. 9: November temperature isotherms at 5 m, 1983- 1988

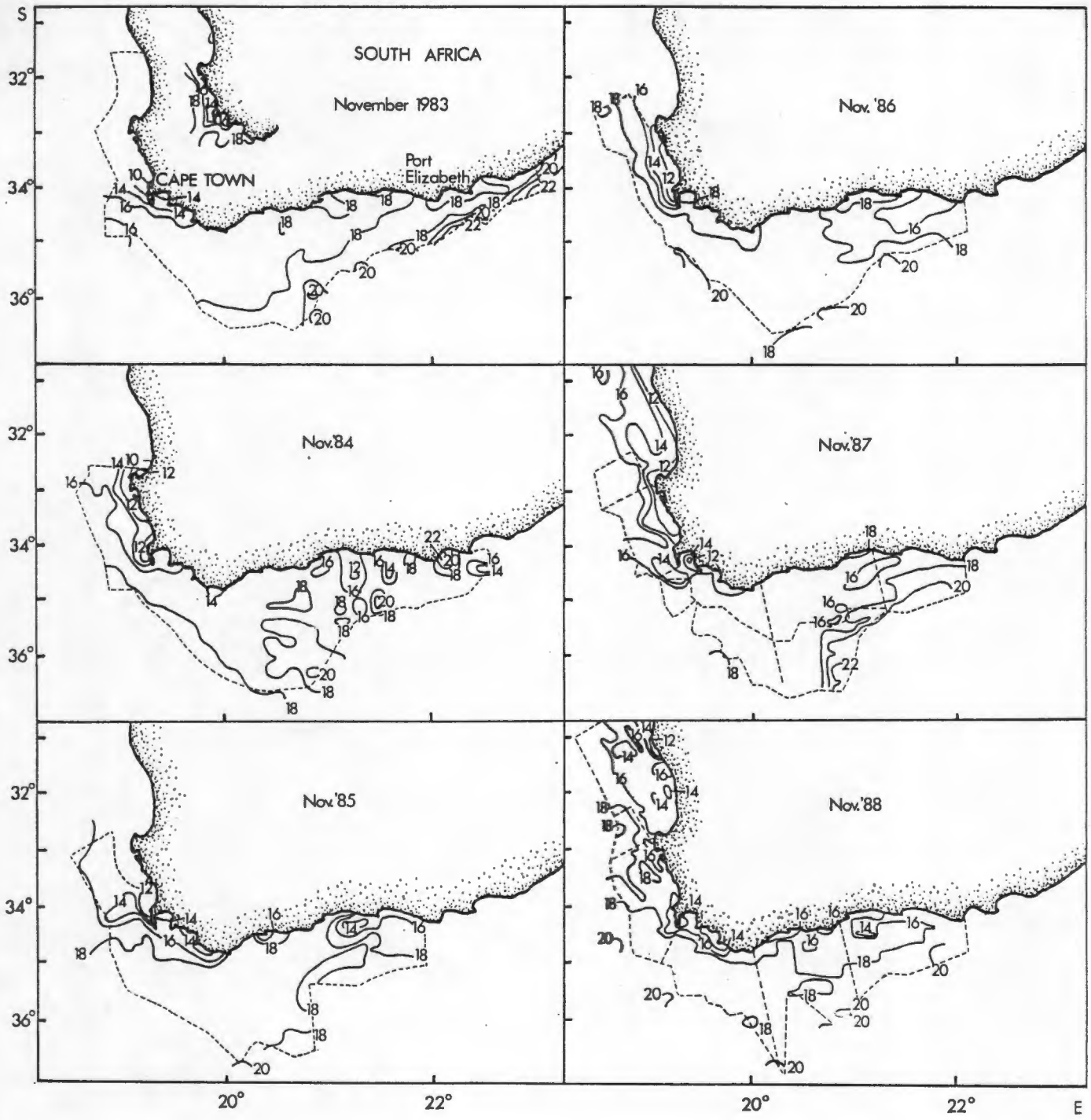


Fig. 10: Anchovy egg distribution during November of 1983-1988

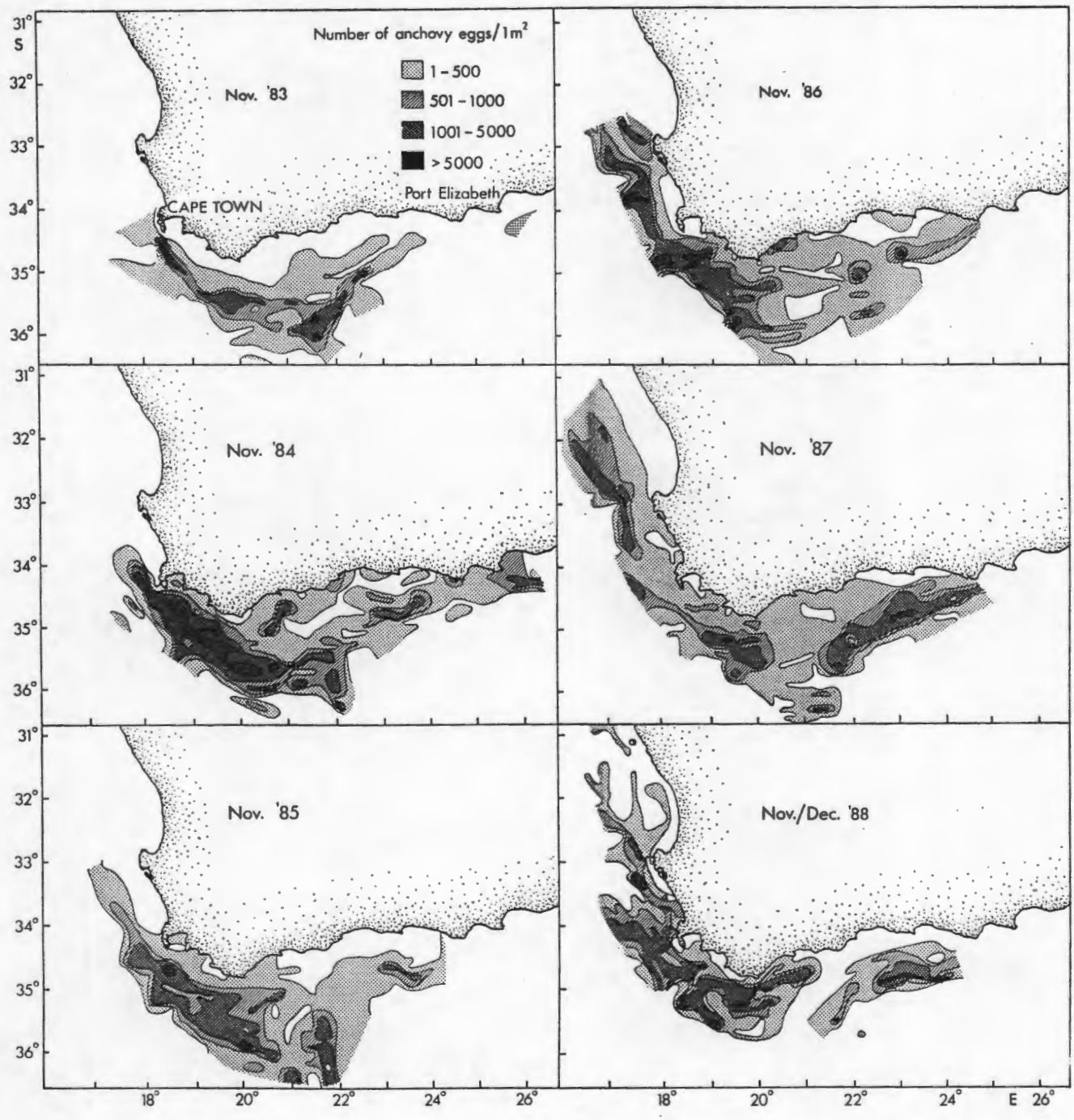
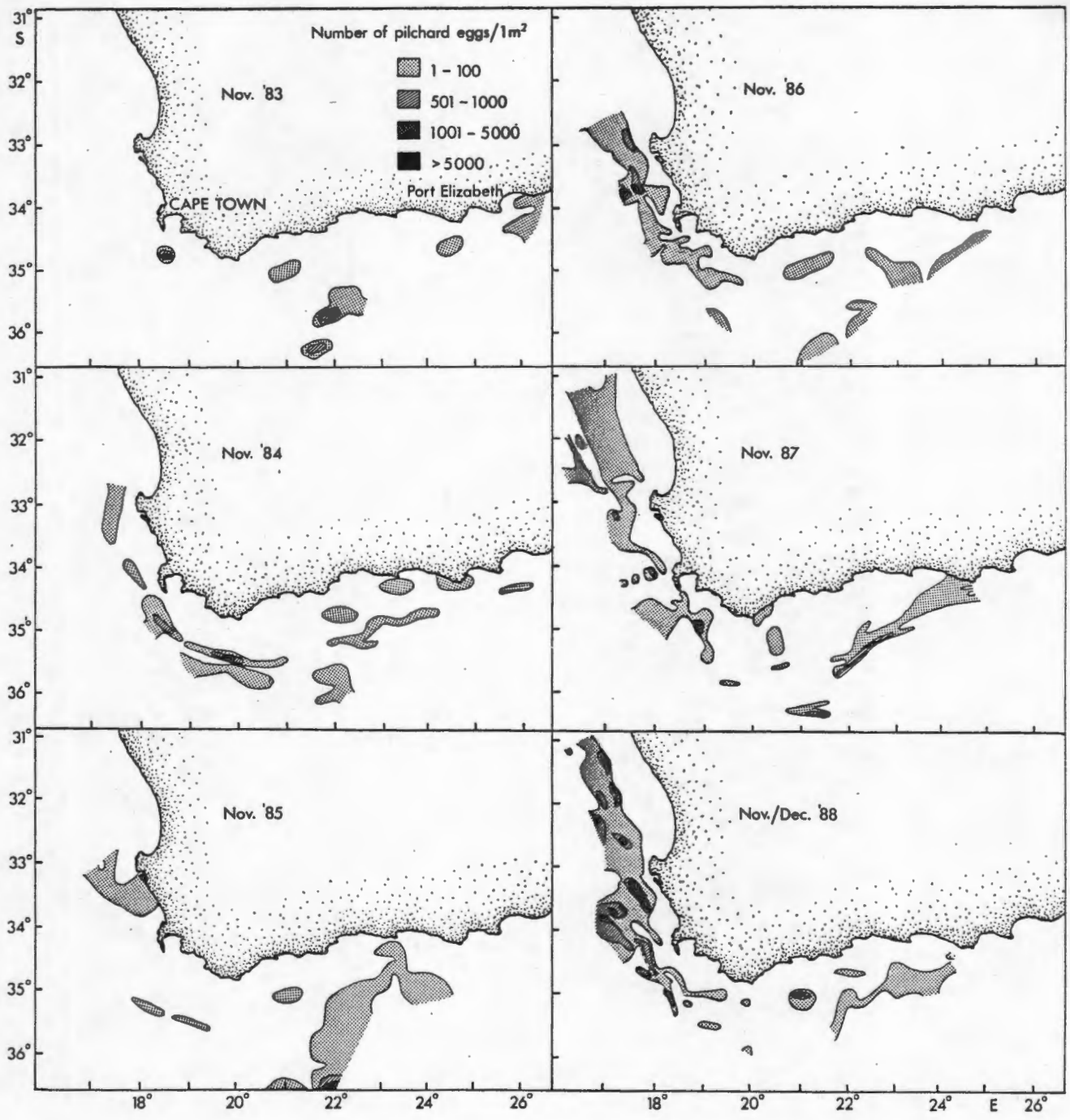


Fig. 11: Sardine egg distribution during November of 1983-1988



egg population. In general terms, there was a good correspondence between the computed values of Q for each year and the observed oceanographic conditions, which may determine the areas normally inhabited by the anchovy and sardine.

The objective here was to document the possible importance of cannibalism and intraguild predation (IGP) in determining the levels of anchovy recruitment. A "guild" (as defined by Polis *et al.* 1989), represents a group of animals (e.g. clupeoids such as anchovy and sardine) which utilize similar resources (food or space) and thus may compete, regardless of differences in tactics of resource acquisition. It is evident that invasion by sardine of areas previously occupied by anchovy may increase the predation pressure on anchovy eggs and larvae and could result in a greater mortality of those early stages.

Data on egg consumption by sardine at stations where both species are found show that sardine predation is potentially more important to anchovy egg mortality than egg cannibalism (see Chapter 5). In 1986, anchovy egg consumption by cannibalism represented only 2% of the total anchovy egg production whereas anchovy egg consumption by sardines represented 6% of the total anchovy egg production (Chapter 5). Therefore, sardine consumption of anchovy eggs in 1986 was about three times greater than anchovy cannibalism, even though sardine biomass was ten times lower than that of anchovy (Armstrong et al. in prep.).

The impact of sardine predation on anchovy eggs may depend on the one hand on the density of anchovy eggs, and on the other on the predator's numerical response (Murdoch, 1969; Murdoch *et al.* 1975). Thus, when sardine stock increases, more depletion of the anchovy stock size could occur because of sardine predation on anchovy eggs. This interaction between both species provides support for the inclusion of the term for compensatory mortality according to size and concentration of sardine and overlapping of both species (Equation 5).

Polis et al. (1989) emphasised that species which suffer intraguild predation (IGP) often exhibit different distribution patterns in space and/or time than their intraguild (IG) predators. Such patterns may be an evolutionary response, a short-term behavioral response to avoid IGP, or simply a reflection of mortality due to IGP. In anchovy and sardine, it may explain the shifts normally exhibited by these species in space and time in the Benguela and similar ecosystems.

In general, the multi-dimensional plot of the stock-recruitment curves for several concentration levels and overlapping indices (Fig. 8) shows that the anchovy population appears as a saturated population when the index of overlapping is constant and is highly concentrated, or when its IG predators are highly concentrated, producing poor recruitments. If all else is equal, sardine will have a greater impact on anchovy recruitment than anchovy

(c > b). According to the model, a decrease in Q_1, Q_2 and O_2 may lead to either a decrease or an increase in the abundance of eggs, depending on the sardine biomass and hence on the relative importance of intraguild predation and intraspecific predation on anchovy eggs at the time.

Results from the model (Fig. 8) show that higher concentration coefficients (Q_1, Q_2) and higher index of overlapping (O_2), like those exhibited in 1986 (Tables I and II), may cause an increase in recruitment, as observed in 1986 given the low sardine stock size. Despite an increase in overlapping with anchovy, either an increase or steady state in concentration coefficients (Q_1, Q_2), may paradoxically increase the abundance of their IG prey, given a sufficient compensatory response by the IG prey to decreased intraspecific competition (S. Cortwright in Polis *et al.* 1989). In 1986, only 2% and 6% of the total anchovy egg production was being consumed by cannibals and IG predators respectively (Chapter 5). This may be the compensatory response to an increased index of overlapping and hence, decreased intraspecific predation (ie. cannibalism) which at that abundance levels was the main density-dependent compensatory mechanism.

In 1987 and 1988 Q values and the index of overlapping (O_2) decreased (Tables I and II) but there was an exponential increase in the absolute number of sardine eggs (Fig. 5) and a decrease in

the number of anchovy eggs (Fig. 4). Figure 5 indicates clearly that sardine tended to crowd current areas of distribution before colonizing new areas. However, because of the enlargement of the sardine stock (during 1987 and 1988) and its crowding at specific spots, anchovy egg survival was greatly affected in areas of high anchovy egg densities and thus, in spite of the lower Q coefficients and index of overlapping, the sardine increase may explain the anchovy egg survival decrease and thus, the lower anchovy recruitment for 1988 (Chapter 5).

In conclusion, the output of the model used in this paper shows that when there is an interaction of species, the degree of overlapping needs to be considered, together with concentration levels and abundances of prey and potential predators, because intraspecific as well as interspecific density-dependent mechanisms may cause synergistic effects in the anchovy recruitment. The results obtained here emphasise the importance of identifying density-dependent mechanisms, such as anchovy egg cannibalism and anchovy egg predation by sardines, which give an indication of an IG interaction between the two species. Such interactions potentially determine anchovy recruitment and should be used as part of a multispecies management plan for the guild interacting species.

ACKNOWLEDGEMENTS

I thank Dr. K Cochrane and Dr. A. I. L. Payne of the Sea Fisheries Research Institute (SFRI), Dr. M. Bergh of the University of Cape Town (UCT), Dr. J. Alheit (Polarmar, Bremerhaven) and my supervisor Professor C. Griffiths (UCT) for many useful discussions and review of the various versions of this manuscript. I also thank the participating scientists, technical staff, the Master, officers and crew of R.S. *Africana* for assistance in data collection. The reprographic section of the SFRI is acknowledged for the artwork. The work is being submitted in partial fulfilment of the requirements of a Ph.D. degree at the University of Cape Town.

REFERENCES

ALHEIT, J. 1987 - Egg cannibalism versus egg predation: their significance in anchovies. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 467-470.

ARMSTRONG, M.J., SHELTON, P.A., HAMPTON, I., JOLLY, G. and Y.C. MELO 1988 - Egg production estimates of anchovy biomass in the southern Benguela system. *Rep. Calif. coop. oceanic Fish. Invest.* 29: 137-157.

ARMSTRONG, M.J., BUTTERWORTH, D.S., HAMPTON, I., PAYNE, B.A., PUNT, A. and P.A. SHELTON (in preparation) - Survey-based management of the multi-species pelagic clupeoid fishery of the southern Benguela upwelling system.

BAKUN, A. 1985 - Comparative studies and the recruitment problem: searching for generalizations. *Rep. Calif. coop. oceanic Fish. Invest.* 26: 30-40.

BAKUN, A., BEYER, J., PAULY, D., POPE, J.G. and G.D. SHARP 1982 - Ocean sciences in relation to living marine resources: a report. *Can. J. Fish. aquat. Sci.* 39(7): 1059-1070.

BUTLER, J.L. and D. PICKETT 1988 - Age-specific vulnerability of Pacific sardine, *Sardinops sagax,* larvae to predation by northern anchovy, *Engraulis mordax. Fishery Bull. Wash.* **86**(1): 163-167.

BROWNELL, C.L. 1985 - Laboratory analysis of cannibalism bylarvae of the Cape anchovy *Engraulis capensis. Trans. Am. Fish. Soc.* **114**(4): 512-518.

BROWNELL, C.L. 1987 - Cannibalistic interactions among young anchovy: a first attempt to apply laboratory behavioural observations to the field. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 503-511.

CLARK, F.N. and J.C. MARR 1955 - Population dynamics of the Pacific sardine. *Prog. Rep. Calif. coop. oceanic Fish. Invest.* **1 July 1953 to 31 March 1955**: 11-48.

CRAWFORD, R.J.M. 1981a - Distribution, availability and movements of anchovy *Engraulis capensis* off South Africa, 1964 - 1976. *Fish. Bull. S. Afr.* **14**: 51-94.

CRAWFORD, R.J.M. 1981b - Distribution, availability and movements of pilchard *Sardinops ocellata* off South Africa, 1964-1976. *Fish. Bull. S. Afr.* **14**: 1-46.

CRAWFORD, R.J.M., SHELTON, P.A. and L. HUTCHINGS 1983 - Aspects of variability of some neritic stocks in the southern Benguela system. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose*, Costa Rica, April 1983. Sharp, G.D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(2): 407-448.

CRAWFORD, R.J.M., SIEGFRIED, W.R., SHANNON, L.V., VILLACASTIN-HERRERO, C.A. and L.G. UNDERHILL 1990 (in press) - Environmental influences on marine biota off southern Africa. *S. Afr. J. Sci.*

CSIRKE, J. 1980 - Recruitment in the Peruvian anchovy and its dependence on the adult population. *Rapp. P-v. Reun. Cons. perm. int. Explor. Mer* **177**: 307-313.

CUSHING, D.H. 1972 - The production cycle and the numbers of marine fish. Symp. zool. Soc. Lond. **29**: 213-232.

CUSHING, D.H. 1975 - *Marine Ecology and Fisheries.* Cambridge. University Press: 278 pp.

GLANTZ, M.H. 1984 - Report of the Working Group on Societal Implications of Varying Fishery Resources. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose, Costa*

Rica, April 1983. Sharp, G.D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* 291(1): 55-56.

GLANTZ, M.H., KATZ, R. and M. KRENZ (Eds) 1987 - The societal impacts associated with the 1982-1983 worldwide climate anomalies. United Nations Environment Programme, Boulder, Colorado; Environmental and Societal Impacts Group, National Center for Atmoshperic Research. 105pp.

GULLAND, J.A. 1977 - Clupeoids. In *Fish Population Dynamics.* Gulland, J.A. (Ed.). London; Wiley-Interscience: 283-308.

GULLAND, J.A. and S. GARCIA 1984 - Observed patterns in multispecies fisheries. In *Exploitation of Marine Communities.* May, R.M. (Ed.). Berlin; Springer: 155-190 (Report of the Dahlem Workshop on Exploitation of Marine Communities, Berlin, April 1984).

HAMPTON, I. 1987 - Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. In *The Benguela and Comparable Ecosystems.* Payne, A.I.L., Gulland, J. A. and K.H. Brink (Eds.). *S. Afr. J. mar. Sci.* 5: 901-917.

HJORT, J. 1914 - The fluctuations in the great fisheries of northern Europe viewed in the light of biological research.

Rapp. P-v. Reun. Cons. perm. int. Explor. Mer **20**: 228 pp.

HUNTER, J.R. 1981 - Feeding ecology and predation of marine fish larvae. In *Marine Fish Larvae*. Lasker, R. (Ed.). Washington, D.C.; Washington Sea Grant Program: 33-77.

HUNTER, J.R. 1984 - Inferences regarding predation on the early life stages of cod and other fishes. In *The Propagation of Cod*. Dahl, E., Danielssen, D., Moksness E. and P. Solemdal (Eds). *Flodevigen Rapportseries*. 1: 533-562.

HUNTER, J.R. and C.A. KIMBRELL 1980 - Egg cannibalism in the northern anchovy, *Engraulis mordax*. *Fishery Bull., Wash.* **78**(3): 811-816.

KAWASAKI, T. 1983 - Why do some fishes have wide fluctuations in their numbers? - Biological basis of fluctuation from the viewpoint of evolutionary ecology. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose, Costa Rica, April 1983*. Sharp, G.D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(3): 1065-1080.

KOSLOW, J.A. 1984 - Recruitment patterns in northwest Atlantic fish stocks. *Can. J. Fish. aquat. Sci.* **41**: 1722-1729.

LASKER, R. 1975 - Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fishery Bull., Wash.* 73(3): 453-462.

LASKER, R. and A. MacCALL 1983 - New ideas on the fluctuations of the clupeoid stocks off California. In *Proceedings of the Joint Oceanographic Assembly, 1982. General Symposia*: 110-120.

MacCALL, A.D. 1976 - Density dependence of catchability coefficient in the California Pacific sardine, *Sardinops sagax caerulea*, purse seine fishery. Rep. *Calif. coop. oceanic Fish. Inves t.* 18: 136-148.

MacCALL, A.D. 1981 - The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis*. In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, 1980*. Sharp, G.D. (Conv. Ed.). Paris; Unesco: 201-220 (*I.O.C. Workshop Rep.* 28).

MERCER, M.C. (Ed.) 1982 - Multispecies approaches to fishery management advice. *Can. spec. Publ. Fish. aquat. Sci.* 59: 169 pp.

MURDOCH, W.W. 1969 - Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39: 335-354.

MURDOCH, W.W., AVERY, S. and SMYTH, M.E.B. 1975 - Switching in predatory fish. *Ecology* 10: 338-342.

MURPHY, G.I. 1967 - Vital statistics of the Pacific sardine *(Sardinops caerulea)* and the population consequences. *Ecology* 48: 731-735.

MURPHY, G.I. 1977 - Clupeoids. In *Fish Population Dynamics.* Gulland, J.A. (Ed.). London; Wiley-Interscience: 283-308.

O'TOOLE, M.J., ARMSTRONG, M.J. and I.HAMPTON (in preparation) - Observations on cannibalism by the South African anchovy (*Engraulis capensis*) on post-larvae and early juveniles.

PALOHEIMO, J.E. and L.M. DICKIE 1964 - Abundance and fishing success. *Rapp. P-v. Reun. Cons. Perm. int. Explor. Mer* 164: 302-315.

PARRISH, R.H., NELSON, C.S. and A. BAKUN 1981 - Transport mechanisms and reproductive success of fishes in the California Current. *Biol. Oceanogr.* 1(2): 175-203.

PETERSON, W.T. and L. HUTCHINGS 1989 - Chlorophyll, particle spectra, zooplankton biomass and production in relation to hydrography and anchovy spawners on the Agulhas Bank. In *Proceedings of the Plankton Dynamics Mini-symposium, Cape Town, South Africa, May 1989. B.E.P. Rep.* 17: 81-95.

POLIS, G.A., MYERS, A. and R.D. HOLT 1989 - The ecology and evolution of intraguild predation: potential competitors that eat each other. *A. Rev. Ecol. Syst.* 20: 297-330.

RICKER, W.E. 1954 - Stock and recruitment. *J. Fish. Res. Bd Can.* 11: 559-623.

RICKER, W.E. 1958 - Handbook of computation for biological statistics of fish population. *Bull. Fish. Res. Bd. Can.* 119: 300 pp.

ROTHSCHILD, B.J. 1986 - Dynamics of marine fish populations. Cambridge, Massachusetts; Harvard University Press: 277 pp.

SANTANDER, H., ALHEIT, J., MacCALL, A.D. and A. ALAMO 1983 - Egg mortality of the Peruvian anchovy (*Engraulis ringens*) caused by cannibalism and predation by sardines (*Sardinops sagax*). In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose, Costa Rica, April 1983.* Sharp, G.D. and

J. Csirke (Eds). *F.A.O. Fish. Rep.* 291(3): 1012-1025.

SAS INSTITUTE INC. 1982 - *SAS User's Guide: Statistics.* Cary, North Carolina; SAS Institute Inc.: 584 pp.

SHANNON, L.V., CRAWFORD, R.J.M., BRUNDRIT, G.B. and L.G. UNDERHILL 1988 - Responses of fish populations in the Benguela ecosystem to environmental change. *J. Cons. perm. int. Explor. Mer* 45(1): 5-12.

SHELTON, P.A., BOYD, A.J. and M.J. ARMSTRONG 1985 - The influence of large-scale environmental processes on neritic fish populations in the Benguela Current system. *Rep. Calif. coop. oceanic Fish. Invest.* 26: 72-92.

SHELTON, P.A. and L. HUTCHINGS 1982 - Transport of anchovy, *Engraulis capensis* Gilchrist, eggs and early larvae by a frontal jet current. *J. Cons. perm. int. Explor. Mer* 40(2): 185-198.

SHEPHERD, J.G. and D.H. CUSHING 1980 - A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment-relationship. *J. Cons. perm. int. Explor. Mer* 39: 160-167.

SHEPHERD, J.G., POPE, J.G. and R.D. COUSENS 1984 - Variations in

fish stocks and hypotheses concerning their links with climate. Rapp. P-v. Reun. *Cons. perm. int. Explor. Mer* 185: 255-267.

SINCLAIR, M. and M.J. TREMBLAY 1984 - Timing of spawning of Atlantic herring (*Clupea harengus harengus*) populations and the match-mismatch theory. *Can. J. Fish. aquat. Sci.* 41(7): 1055-1065.

SISSENWINE, M.P. 1984 - Why do fish populations vary? In *Exploitation of Marine Communities*. May, R.M. (Ed.). Berlin, Springer: 59-94 (Report of the Dahlem Workshop on Exploitation of Marine Communities, Berlin, April 1984).

SKUD, B.E. 1982 - Dominance in fishes: the relation between environment and abundance. *Science, N.Y.* 216(4542): 144-149.

SMITH, P.E., FLERX, W. and R.P. HEWITT 1985 - The CalCOFI vertical egg tow (CalVET) net. In *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, Engraulis mordax*. Lasker, R. (Ed.). Tech. Rep. NOAA NMFS 36: 27-32.

SOUTAR, A. and J.D. ISAACS 1969 - History of fish populations inferred from fish scales in anaerobic sediments off California. *Rep. Calif. coop. oceanic Fish. Invest.* 13: 63-70.

SOUTAR, A. and J.D. ISAACS 1974 - Abundance of pelagic fish during the 19th and 20th centuries as recorded in anaerobic sediment off the Californias. *Fishery Bull., Wash.* 72: 257-273.

VALDES, E. 1986 - Egg cannibalism by anchovy in the Southern Benguela Current region. M.Sc thesis. University of Cape Town: 85 pp.

VALDES, E.S., SHELTON, P.A., ARMSTRONG, M.J. and J.G. FIELD 1987 Cannibalism in South African anchovy: egg mortality and egg consumption rates. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 613-622.

WALTERS, C.J. 1984 - Managing fisheries under biological uncertainty. In *Exploitation of Marine Communities*. May, R.M. (Ed.). Berlin; Springer: 263-274 (Report of the Dahlem Workshop on Exploitation of Marine Communities, Berlin, April 1984).

WARE, D.M. 1975 - Relation between egg size, growth, and natural mortality of larval fish. *J. Fish. Res. Bd Can.* 32: 2503-2515.

WHITE, P.N. 1988 - Clupeoid piscivory and year class strength. In *Benguela Clupeoid Piscivory (Research Project 1987/1988)*. Unpublished internal report, Dept of Zoology, University of Cape Town: 4 pp.

C H A P T E R 3

Manuscript submitted to the Proceedings of the Symposium: "Trophic Functioning of the Benguela System", held in Cape Town on 22 to 25 August, 1989

ESTIMATES OF THE ANNUAL CONSUMPTION OF FOOD BY ANCHOVY AND OTHER PELAGIC FISH SPECIES OFF SOUTH AFRICA DURING THE PERIOD 1984-1988

M.J. ARMSTRONG[1], A.G. JAMES[2] and E.S. VALDES[3]

1. Aquatic Sciences Research Division, Newforge Lane, Belfast BT9 5PX, Northern Ireland

2. Formerly Sea Fisheries Research Institute, Private Bag X2, Rogge Bay, 8012, Republic of South Africa

3. Sea Fisheries Research Institute, Private Bag X2, Rogge Bay, 8012, Republic of South Africa

This paper provides information on abundance, diet and food consumption rate of anchovy Engraulis capensis from data collected during routine acoustic surveys that took place off the coast of South Africa during the years 1983-1988. Separate estimates are made of the quantities of phytoplankton and micro-, meso- and macro-zooplankton consumed by the anchovy population off the West and South Coasts, for inclusion in the network analyses of carbon flow through the foodweb of the southern Benguela system reported by Cochrane (this volume). These estimates replace those given by Shannon and Field (1985) and Bergh et al. (1984) as they are based on much more accurate data; however in view of the large variation in the data, the sources of error are discussed in some detail.

Hampton (1987) and Hampton *et al.* (in prep) give detailed information on the distribution and abundance of anchovy off South Africa from the results of acoustic surveys carried out off the West Coast in winter and off the South and West Coasts in spring/summer. These are snapshots of a dynamic seasonal pattern of abundance and distribution that must be simulated if meaningful estimates of the total consumption of food by anchovy off the West and South Coasts are to be obtained. In order to simulate these patterns, the growth in biomass of each recruiting year class over the period 1984-1988 was reconstructed from estimates of natural mortality rate *M* (Butterworth, University of Cape Town, unpublished) and somatic growth (Waldron *et al.* 1989), and of rates of emigration from the West to the South Coast inferred from changes in distribution of anchovy between winter and summer cruises. These reconstructions provided estimates of monthly biomass off the West and South Coasts during each of the years investigated. An illustration of the distribution ranges of juvenile and adult anchovy is given in Figures 1 and 2.

The anchovy provides a case study because of the detailed information available from acoustic surveys directed at this species. Considerably poorer data (or none at all) are available to allow estimates of food consumption by the other abundant shelf-dwelling pelagic fish *viz.* pilchard *Sardinops ocellatus*,

Fig. 1. Distribution of juvenile anchovy deduced from echo-integration and midwater trawling during June 1986 (adapted from Hampton 1986).

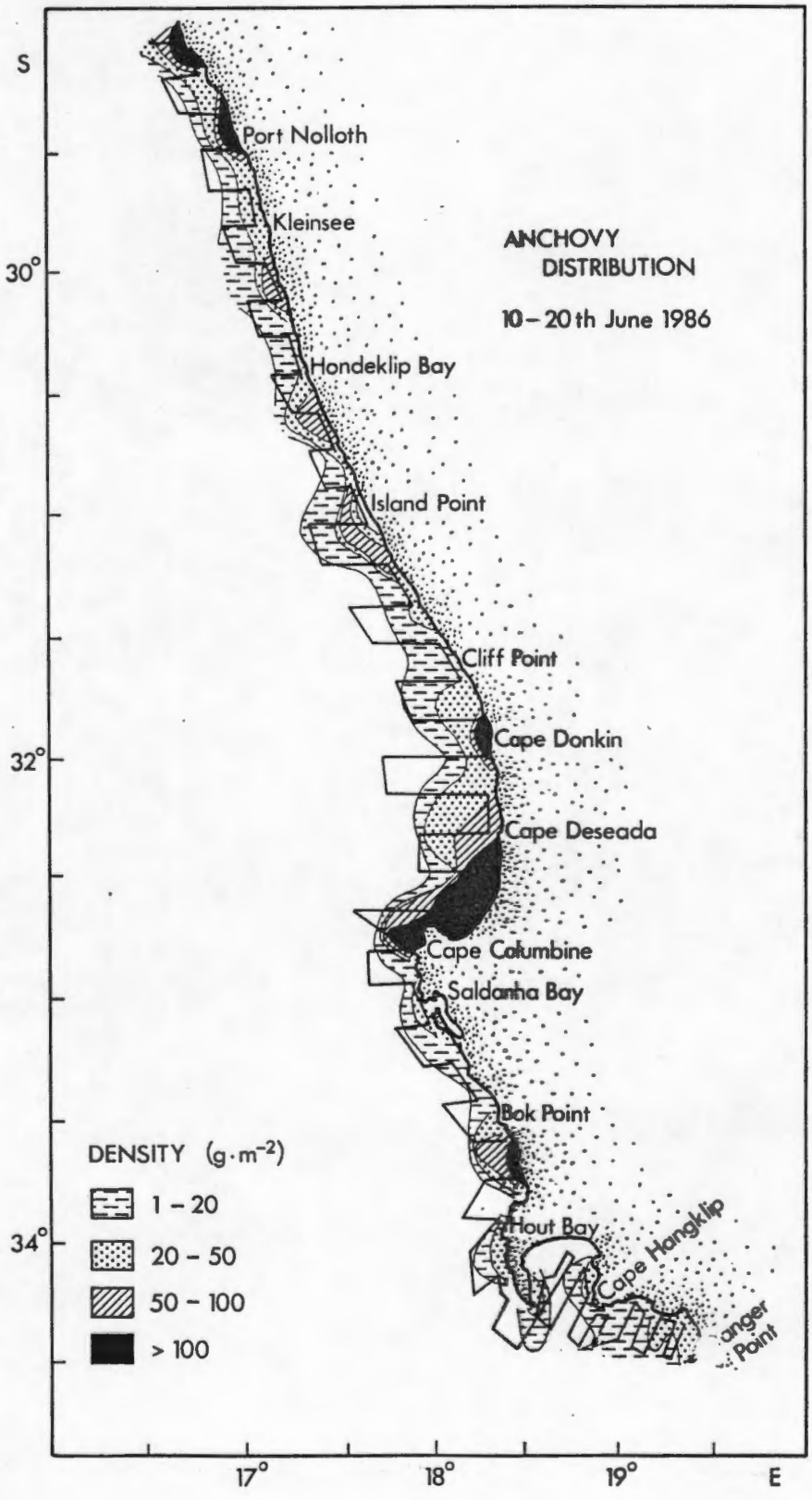
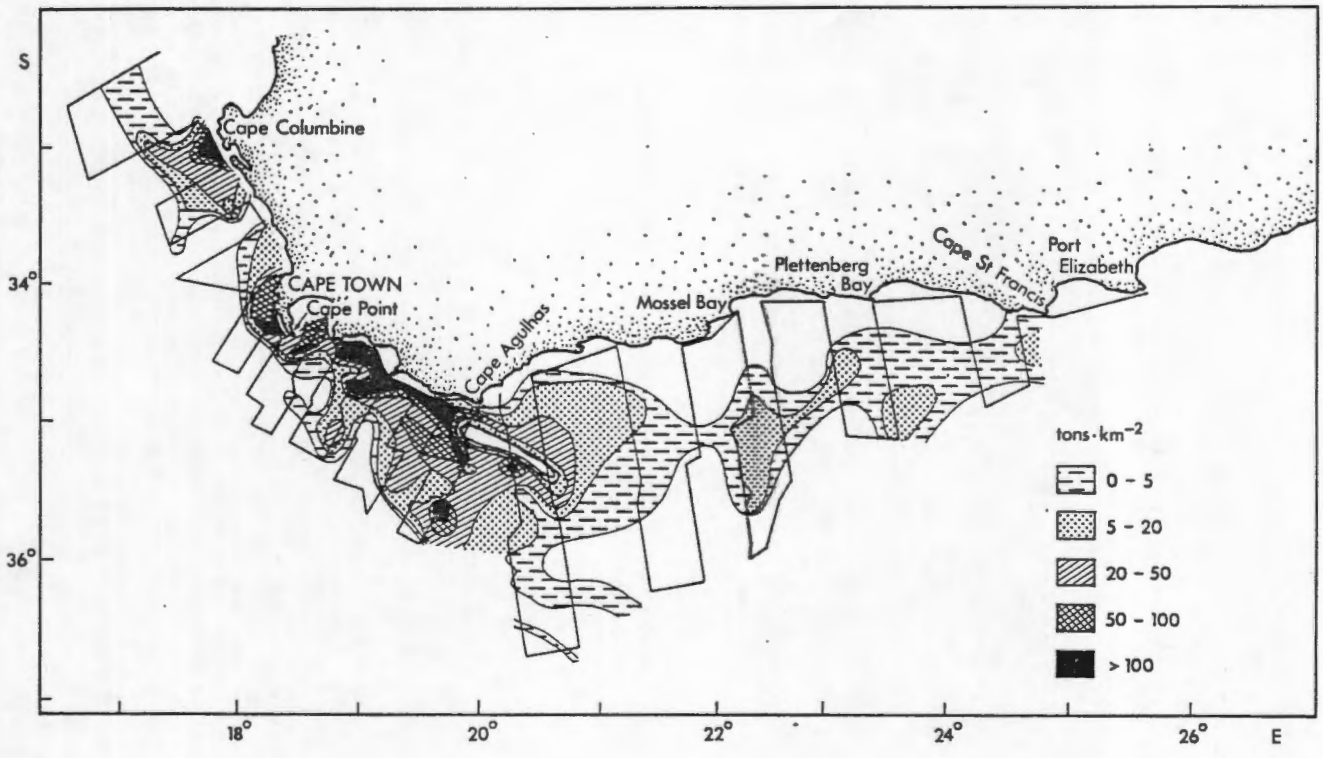


Fig. 2. Distribution of adult anchovy deduced from echo-integration and midwater trawling during November 1986.



round herring Etrumeus whiteheadi, lanternfish Lampanyctodes hectoris and lightfish Maurolicus muelleri. Those data that have been obtained as a by-product of the routine acoustic surveys of the anchovy population are summarized.

SEASONAL TRENDS IN ABUNDANCE OF ANCHOVY

Juvenile anchovy occupy a narrow coastal belt along the West Coast and South-west coasts. While they are retained in this belt they grow at a rate of almost 1 cm.month^{-1} (Waldron et al. 1989) and the southward migration of juveniles takes them towards spawning grounds off the South-west and South coasts. Acoustic surveys of anchovy juveniles have taken place from May to July of the years 1983 - 1990 and have shown that at this time the great majority of the juveniles are still present off the West Coast (Hampton 1987, Hampton and Armstrong in prep., Fig. 1). By November, most of the juveniles have attained maturity and have migrated onto the South Coast (Fig. 2). During acoustic surveys of the West and South Coasts in November 1983, 1984 and 1985, no significant quantities of anchovy were detected in the regions of the West Coast that were surveyed (Hampton 1987), indicating that all the recruiting fish may have migrated onto the South Coast. In contrast, surveys during November 1986, 1987 and 1988, and in February 1987, showed high densities of anchovy off the West Coast (Fig. 2, Table I, Hampton and Armstrong in prep.), coinciding with a period of high

Table I: Relative occurrence of the anchovy population off the West and South Coasts during summer, as inferred from estimates of biomass in each region during acoustic surveys from 1984 to 1989.

Survey	Percentage of estimated total biomass	
	West Coast	South Coast
November 1984	0	100
November 1985	0	100
November 1986	7,2	92,8
February 1987	17,8	82,2
November 1987	37,8	62,2
November 1988	16,8	83,2
November 1989	11,9	88,1

catches of adult fish by purse-seiners operating in that region.

Changes in abundance of individual cohorts

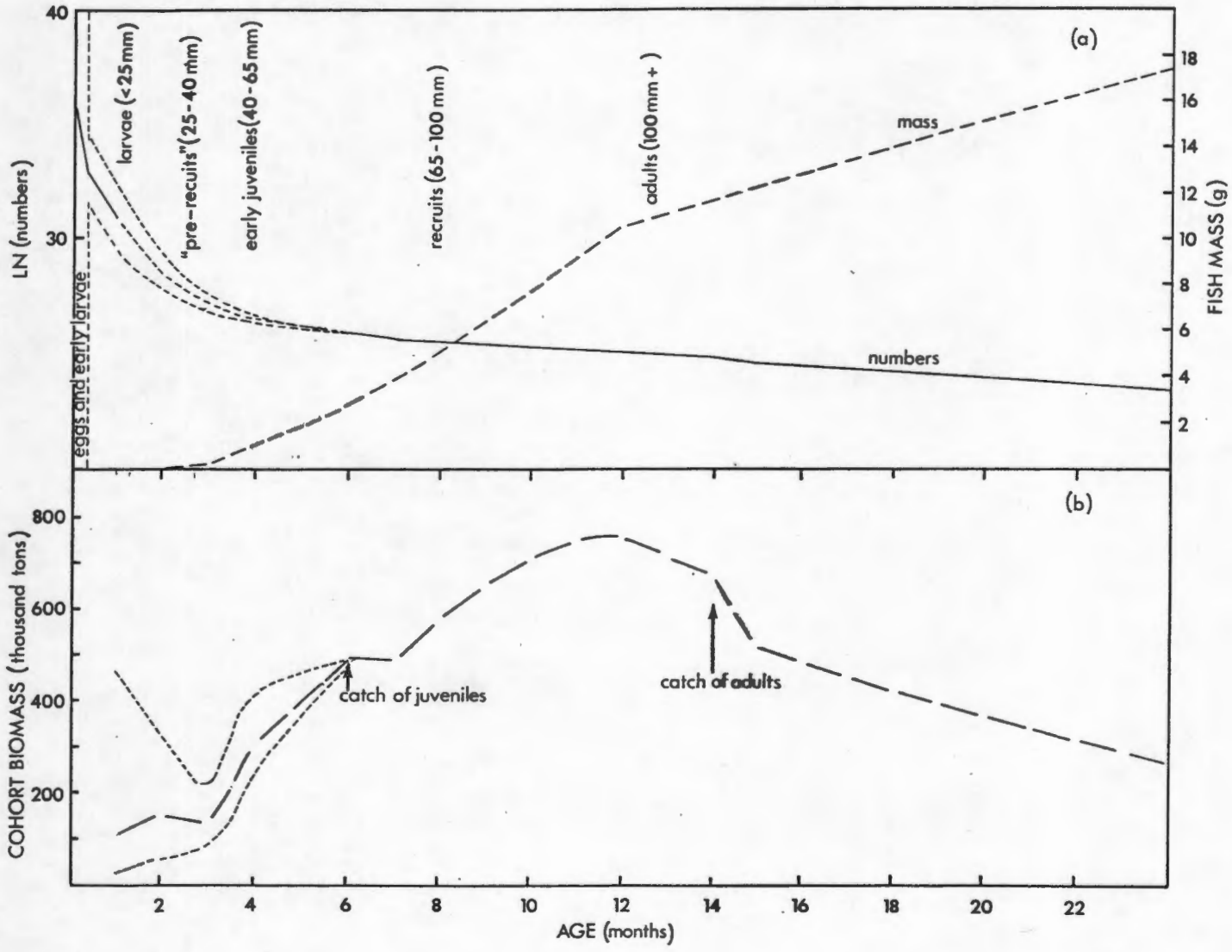
JUVENILES AND ADULTS

The abundances and rate of decline from six months of age of anchovy of the 1984-1988 year classes were estimated by means of a pseudo-Bayesian estimation procedure (Bergh and Butterworth, 1987), applied to catch and survey data for the period 1983 - 1990 (Butterworth, University of Cape Town, unpublished). This procedure was devised to provide maximum-likelihood estimates of mean recruitment and instantaneous rate of natural mortality $\underline{M}$ for the purposes of making prognoses of future stock sizes of anchovy under different catch levels, as required for management of the fishery. As it is assumed that $\underline{M}$ is year- and age-invariant, and that recruitment fluctuates randomly about a fixed average, the estimated variation in abundance of individual year-classes is likely to be damped. However, as the average abundance over a five-year period is of interest here, this feature is of relatively little concern. The estimate of $\underline{M}$ for juvenile and adult mortality, obtained from this procedure, was 1,33 yr^{-1} (0,11 mo^{-1}, Butterworth, University of Cape Town, unpublished).

Growth in mass of individual anchovy was inferred from data collected during acoustic surveys at the peak of the spawning season in November 1985, 1986, 1987 and 1988. The average masses

of fish attaining one, two and three years of age during these surveys were 10,5, 17,5 and 22,0 g respectively. In the absence of any information on seasonal variations, growth in mass from one to two years of age and from two to three years of age was assumed to be linear. The growth in mass of juveniles was estimated from the results of daily growth studies of the 1985 and 1986 year classes of anchovy reported by Waldron *et al.* (1989). The Von Bertalanffy curve fitted by the latter authors to data from the 1985 year class was scaled to give a length at one year of age of 10 cm caudal length (L_c). This was considered to be the most likely mean length of anchovy at one year of age during the years 1984-1988, given the apparent decline in growth of juveniles over the period 1985-1989 reported by Waldron *et al.* (in prep.). Lengths at ages less than one year were obtained from the adjusted growth curve, and converted to mass by the expression $W = 0,0105.L^3$ where W is the mass in g and L is the caudal length in cm. The latter expression was derived for an expected mass of 10,5 g (i.e. the mean mass of 1-yr-old anchovy during surveys at the peak of the spawning season in November) at a caudal length of 10 cm, assuming an exponent of 3,0. The resultant pattern of growth in mass of juveniles and adults is shown in Figure 3a, together with the average pattern of decline in the logarithm of numbers of fish of the 1984-1988 year-classes from six months of age at the estimated natural mortality rate of 1,33 yr^{-1}. This curve also reflects the losses due to fishing, assumed to occur as pulses at 0.5 and 1.25 years

Fig. 3. (a) Decline in the logarithm of average number of anchovy of the 1984-1988 year-classes from the egg to 2 years of age, inferred from analysis of acoustic survey and commercial catch data for fish of six months and older, from analysis of egg survey data and from estimates of larval mortality given in the literature. Also shown is the growth in mass of individual anchovy. (b) Average growth in biomass of year-classes of anchovy produced over the period 1984-1988. The dotted curves from zero to six months of age represent biomasses corresponding to the dotted curves in (a).



of age.

The change in biomass of the "average" cohort from six months of age is illustrated in Figure 3b, and shows that after an initial small decline due to the commercial catch, the biomass increased to a peak at some 12 months of age and then declined. The shape of the biomass curve is consistent with the occurrence of first spawning towards the end of the first year of life, as the egg production of the stock would be maximised.

PRE-RECRUITS

The mortality rate of larvae and pre-recruit anchovy must be considerably higher than that of juveniles and adults. The likely magnitude of the biomass of late larvae and pre-recruit anchovy was inferred from egg production data (Armstrong et al. 1987) and data on larval mortality given in the literature. The mean daily egg production of the South African anchovy stock is estimated each November for the purposes of applying the egg production method of estimating biomass (Armstrong et al. op. cit.). Estimates for the period 1984-1988 have been in the range 304-488 eggs.m^{-2}.d^{-1} (mean 364 eggs.m^{-2}.d^{-1}), within a spawning area of 110 000 km^2. For the purposes of estimating average total annual egg production, it was assumed that spawning took place predominantly over the period October to January and that the mean daily egg production rates for the months October, November, December and January of the years under investigation were 182, 364, 364 and 182 eggs.m^{-2}.d^{-1}

respectively. This pattern approximates the seasonal pattern of egg abundance reported by Shelton (1986) from monthly ichthyoplankton surveys carried out off South Africa during the period 1977-1978. The average total annual egg production is thus estimated to be $360*10^{13}$ eggs. The mortality rates of eggs during surveys over the period 1984 - 1989 have averaged approximately 0,01 h^{-1}, or 0,24 d^{-1} (Armstrong et al. 1987, Sea Fisheries Research Institute unpublished data), representing a survival rate of some 55% over the 60-h incubation period.

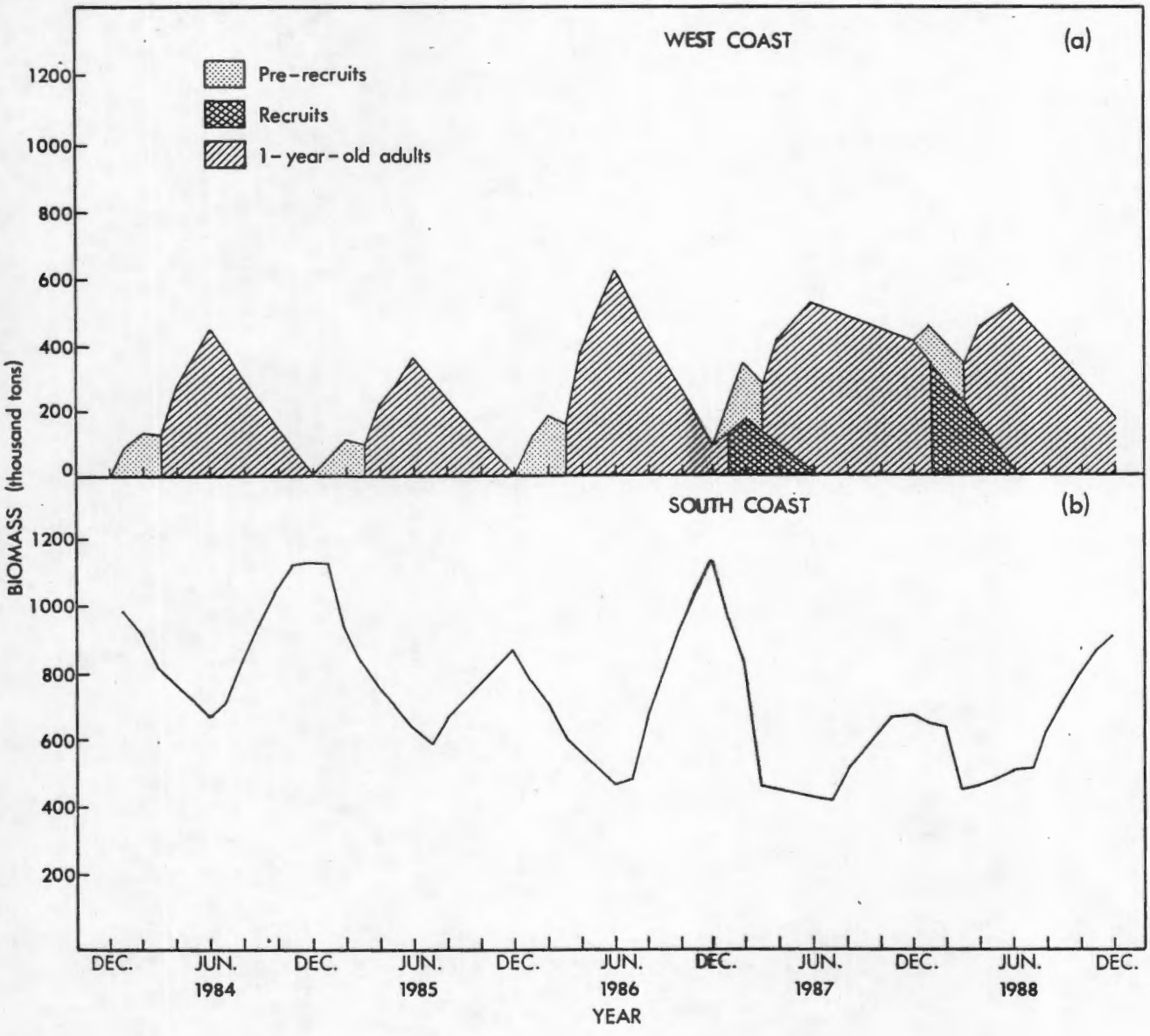
The mortality of early stage larvae is similar to that of eggs, and Lasker (1984) shows that for the northern anchovy Engraulis mordax, the production rate of 10-day-old larvae was on average 5,5 percent the rate estimated for eggs during the years 1980-1983 (i.e. M=0,29 d^{-1}). The mortality rate of E. mordax larvae of 10-20 days old was on average 0,10 d^{-1} (Lasker op. cit.). The decline in night-time catch rates with increasing length of anchovy larvae up to 33 mm sampled off Namibia by Badenhorst and Boyd (1980) also indicated a mortality rate of the order of 0,10 d^{-1}, given the daily growth rates of anchovy larvae reported by Prosch (1986).

In Figure 3a, the average number of eggs and 10-day-old larvae are plotted on a log scale, assuming a value of M of 0,29 d^{-1} over this period (Lasker 1984). The average number of 30-day-old larvae is shown for an assumed M of 0,10 d^{-1} over the range of ages 10-30

days. The dashed line from 1 to 6 months of age on Figure 3a is fitted by eye to give one possibility for a smooth curvilinear decline in the logarithm of the numbers over this range of ages, given the estimate of the average number of 6-month-old fish obtained by means of the Butterworth model. Mortality curves that would be appropriate in the event of a ± 50% error in the estimate of mortality of eggs and early larvae, (or equivalently in the event of the estimated annual egg production being 0,25 or 4,0 times the estimate of $360*10^{13}$ eggs), are also shown. The corresponding growth of biomass during the first six months of life is shown in Figure 3b, and shows a fairly smooth continuation of the curve from that describing the change in biomass between 6 and 12 months of age. Had the annual egg production been considerably larger than estimated, or the egg and larval mortality 50% less than assumed, the biomass of larvae could have attained a level similar to that of 6-month-old fish (upper curve, Fig. 3b), although not as a standing stock.

Figure 4 shows the seasonal variations in total biomass over the period 1984-1988, separately for the West and South Coasts. The biomass values in Figure 4 have been partitioned into West Coast and South Coast components under the assumption that 100% of the recruits are present off the West Coast in June, and that the biomass off the West Coast then declines linearly with time because of emigration to the South Coast. The decline rate due to emigration was adjusted so that the relative abundances of

Fig. 4. Monthly variations in the biomass of anchovy off (a) the West Coast and (b) the South Coast during the period 1984-1988.



fish in each of the regions during spring and summer was as estimated during each of the November surveys and during the February 1987 survey (Table I). Figure 4a indicates a sharp peak in biomass of anchovy on the West Coast occurring around June. From June 1987 to June 1988, the biomass off the West Coast was relatively constant (although considerable spatial variation may have been evident). A strong seasonal pattern also occurs off the South Coast, with the biomass attaining a peak during summer when the fish have migrated onto the spawning grounds. The decline in biomass from summer to winter off the South Coast also coincides with a shift in the distribution of adult fish from the western Agulhas Bank to the eastern Agulhas Bank (Hampton and Armstrong in prep.).

Table II gives annual estimates of biomass of anchovy off the West and South Coasts, obtained as averages of monthly estimates in each of the years 1984-1988. The separate figures given for pre-recruits (1-3 months old) off the West Coast were obtained by extrapolating the numbers of fish in each cohort backwards in time from six months of age. The monthly averages over the five years 1984-1988 were 268 000 t of juveniles and adults for the West Coast (SD=104 000 t), 32 000 t of pre-recruits (SD= 6 700 t) and 723 000 t for the South Coast (SD=121 000 t).

Table II: Estimates of average monthly biomass of anchovy off the West and South Coasts during the years 1984-1988, in thousands of tons. Means and standard deviations (in parenthesis) are given.

	West Coast		South Coast
Year	Pre-recruits	Post-recruits	
1984	30	184	891
1985	23	144	778
1986	41	279	728
1987	36	386	582
1988	32	350	637
Mean	32 (7)	268 (104)	723 (121)

RATE OF FOOD CONSUMPTION BY ANCHOVY

Food supply to the fish

Juvenile anchovy migrating along the West Coast consume phytoplankton and zooplankton that are produced in or advected into the narrow coastal belt occupied by the fish. The mode of feeding (particulate- or filter-feeding) and the consumption rate are determined largely by the concentration and size-spectrum of particles in the water (James and Findlay 1989). These vary considerably along the West Coast in response to upwelling or stabilization of the water column. The anchovy distribution is usually patchy (see Hampton 1987) and persistent aggregations of fish are found in certain regions, particularly in St Helena Bay (see Fig. 1). These aggregations can have an observable impact on local zooplankton densities (Hugget and Painting in prep), and food consumption rates by the anchovy could decline when the local plankton stocks become depleted. The diet of anchovy off the West Coast was investigated during acoustic surveys of this region in May 1983 and in April and May 1984 (see later). The distribution of zooplankton during the May 1983 cruise is given by Verheye and Hutchings (1988).

The distribution of anchovy off the South Coast varies considerably according to the age of the fish and the time of year. High densities of one-year-old fish build up over the western

Agulhas Bank during spring as the juvenile fish migrating from the West Coast become mature and move offshore to spawn (Hampton 1987, Hampton and Armstrong in prep.). The water column in this region becomes intensely stratified in spring and summer (Swart and Largier 1987), and the deep thermoclines result in a production of zooplankton that may be low enough to limit the feeding rate of the anchovy (Hutchings and Peterson in prep.). Rates of egg cannibalism by anchovy can be locally high in this region (Valdes et al. 1987). During summer the anchovy (and other pelagic clupeoids) move shorewards as stratification of the offshore waters becomes more intense and surface temperatures rise above 20^{0}C (Shelton et al. 1985, Payne and Armstrong in prep.). As the temperatures fall from about March onwards, the adult anchovy move slightly offshore and the population shifts eastward to occupy the eastern Agulhas Bank (Crawford 1981, Hampton and Armstrong in prep.). Plankton production during winter is inhibited by lowered light levels and deep mixing of the water column by storms (Shelton et al. 1985), but by November, the two-year-old and older anchovy have moved to the mid- to outer-shelf regions of the eastern Agulhas Bank where shallow thermoclines result in much higher plankton production rates than observed over the Western Agulhas Bank (Hutchings and Peterson in prep.). Feeding rates of anchovy in this region are probably not limited by plankton production rates, and the fish have been observed to have a high fat content relative to those on the western Agulhas Bank (Schulein, Sea Fisheries Research Institute, personal communication). The stomach contents of anchovy

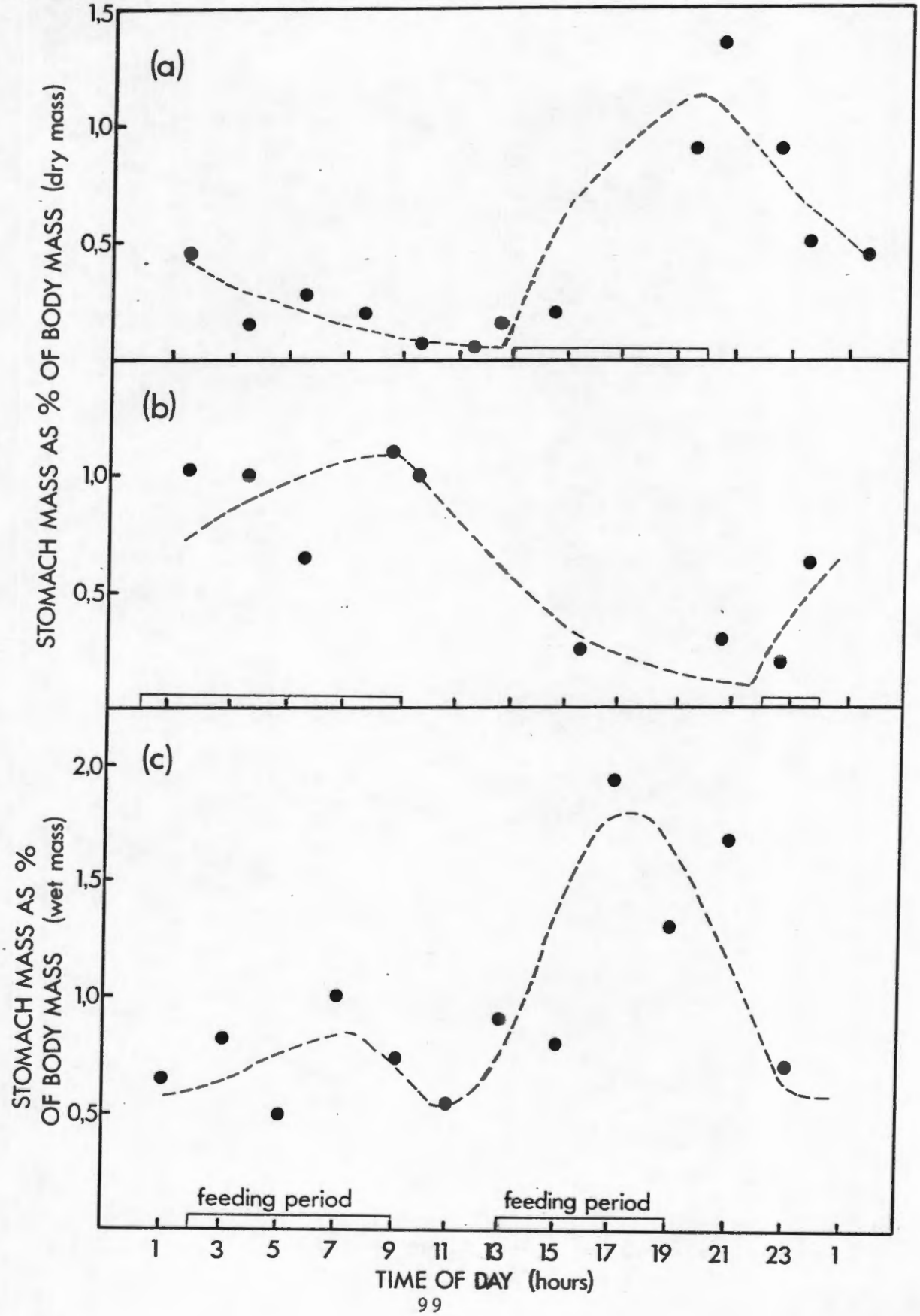
collected off the western and eastern Agulhas Bank during November 1983 were examined to estimate species and size composition of the diet (see later).

Estimation of daily rates of food consumption of anchovy

Estimates of daily rates of food consumption of anchovy off the West Coast were made from field estimates of the ratio of stomach content mass to fish mass ($\underline{W}$) made during cruises in this region during May 1983 and April and May 1984. These data were originally presented by James (1987). Estimates for the South Coast were obtained from data on stomach content masses collected during cruises in November 1983 (James op. cit.) and in November 1986, 1987 and 1988. Data from November 1983 were treated separately from those collected during the subsequent November surveys because of the time gap between surveys and because the diel pattern of feeding was clearly different.

Mean values of $\underline{W}$ in 1-h time strata are shown for the three groups of surveys in Figure 5. The values of $\underline{W}$ are in terms of dry mass for the surveys in 1983 and 1984 (Figs 5a and b), and in wet mass for the surveys in 1986-1988 (Fig. 5c). The data from the West Coast (Fig. 5a) were mostly from the period 20h.00 to 15h.00 the following day and showed high values in the early

Fig. 5. Diel variations in the ratio of stomach content mass to fish mass for anchovy sampled during acoustic surveys in (a) May 1983 and April and May 1984 (data from James 1987), (b) November 1983 (data from James op. cit.) and (c) November 1986, 1987 and 1988. The curves were fitted as described in the text.



evening period before midnight. The values of W appeared to decline exponentially during the late evening and early morning, reaching low values around midday. From these data there appeared to be only one feeding period, occurring during the afternoon and early evening. In contrast, the data for the South Coast in November 1983 (Fig 5b) showed W increasing over the late evening and morning period.

The data from the South Coast during the years 1986-1988 (Fig. 5c) showed a similar pattern to the West Coast data except that there appeared to be a period of low-intensity feeding around dawn as well as a period of intense feeding leading to maximum values of W in the early evening. The latter data indicated two feeding periods, the first occurring from about 02h.00 to 09h.00 and the second from 13h.00 to 19h.00.

A difference-equation model of rates of feeding and gastric evacuation was utilized to simulate the observed diel patterns in W, and was based on an exponential model of stomach evacuation and an assumption that feeding took place at a continuous rate over one or two discrete feeding periods each day. A similar model was constructed by Jarre et al. (1989) and was used to estimate daily food intake of Engraulis ringens. Continuous feeding was simulated as the consumption of identical sized meals at 1-h intervals during each feeding period. It was assumed that the mass of an individual meal does not decline noticeably during the first hour after

ingestion while the digestive juices penetrate the zooplankton carapaces or the diatom frustules. The mass of the stomach contents was assumed to decline with time according to the equations:

for $i = p$ to $p+n-1$:

$$W_{(i+1)} = (W_{(i)} - G) * \exp(-r) + 2G \qquad (1)$$

for $i = p+n$:

$$W_{(i+1)} = (W_{(i)} - G) * \exp(-r) + G \qquad (2)$$

for $i = p$ to $p+n$:

$$W_{(i+1)} = W_{(i)} * \exp(-r) \qquad (3)$$

where:

- i is the time of day (h);
- p is the time of commencement of a feeding period;
- n is the duration of the feeding period (i.e. number of 1-h meals);
- $W_{(i)}$ is the ratio of stomach content mass to fish mass at time i;
- G is the ratio of meal size to mass of fish;
- r is the instantaneous rate of gastric evacuation (h^{-1}).

The data in Figure 5 were considered too noisy to allow the simultaneous estimation of all the parameters related to equations (1) to (3). The evacuation rate r was estimated separately from the

West Coast values of $\underline{W}$ between 19h.00 and 12h.00 the following day, as there appeared to be an exponential decline in stomach mass over this period. The values of $\underline{W}$ were log-transformed and regressed against time of day using the method of least squares. The estimate of $\underline{r}$ was 0,19 (r^2 =0,90; standard error = 0,023). This estimate is not significantly different from a laboratory derived estimate of $\underline{r}$ = 0,227 (SE=0,055) obtained for *E. capensis* fed on *Artemia salina* (James *et al.* 1989), although it is faster than obtained for some other food items presented to the fish by the latter authors. A value of $\underline{r}$ = 0,17 was estimated for juvenile menhaden *Brevoortia tyrannus* fed on copepods by Kjelson *et al*. (1975). As the field estimate of $\underline{r}$ in the present study appeared feasible in the light of laboratory estimates, it was held constant at the value 0,19 h^{-1} and the number and duration of feeding periods, and the size of individual meals ($\underline{G}$), were adjusted iteratively until the following condition was met:

$$(\text{Log } \underline{W}_i - \text{Log } \underline{W}_i')^2 = \text{minimum}$$

where $\underline{W}_i$ = observed mean ratio of stomach mass to fish mass during hour $\underline{i}$; and

$\underline{W}_i'$ = expected ratio for a given set of model parameters, obtained as $(\underline{W}_i + \underline{W}_i+1)/2$.

The values of $\underline{W}_i'$ providing the minimum sum of squares are represented by the curves fitted to the data in Figures 5a-c. The values of the different model parameters, and the estimated daily

food intake, are given in Table III. As the values of W for the surveys in November 1986-1988 are in terms of wet mass, it was necessary to make a conversion to dry mass. James (1987) gives the ratio of dry mass to wet mass for copepods and euphausiids as 0,14-0,16. The equivalent ratio for anchovy is in the range 0,25-0,35 depending on fat content (Sea Fisheries Research Institute, unpublished data). Hence a ratio of dry stomach content mass to dry fish mass for anchovy feeding on zooplankton would be some 50% of the ratio expressed in terms of wet mass.

The estimates of daily intake (dry mass ratios) during the three groups of surveys were very similar, and ranged from 1,73 to 2,16% (mean 1,88%). Using a similar feeding model, Jarre et al. (1989) estimated the daily food intake of Engraulis ringens to be 3,0-3,3% (wet mass ratio), or 1,5-1,65% in terms of dry mass. These values are considerably less than the figure of 10% (wet mass ratio) adopted by Shannon and Field (1984) for estimating the food consumption of the South African anchovy population.

Annual consumption of food by anchovy

The annual consumption of food by anchovy off the West and South Coasts was derived from the estimates of mean biomass over the year and the product of the mean daily rate of consumption of food and the number of days in the year (Table IV). The dry mass

Table III: Estimates of parameters related to the diel pattern of food intake by anchovy described by equations (1)-(3) and illustrated in Figures 5 a-c. Key to surveys: A= May 1983/84 (West Coast); B= November 1983 (South Coast); C= November 1986-1988 (South Coast). Data for survey category C have been converted from wet-mass to dry-mass ratios.

Survey	Time feeding starts	Duration of feeding (h)	Hourly meal size (% body mass)	Daily intake (% body mass)
A	13h.00	8	0,22	1,76
B	22h.00	12	0,18	2,16
C	02h.00	7	0,075	
	13h.00	6	0,200	1,73
Mean				1,88

Table IV: Average annual consumption of food by anchovy off the West and South Coasts over the period 1984-1988. All figures are in thousands of tons.

Coast	Population component	Mean wet biomass	Mean dry biomass	Annual consumption	
				Dry mass	Carbon
West	Pre-recruits	32,4	9,72	66,7	28,0
	Post-recruits	268,0	80,4	551,7	231,7
South	Post-recruits	723,0	216,9	1488,4	625,1

of food consumed per year was converted to tons carbon by means of the carbon content data for copepods and euphausiids given in James (1987). The carbon content of phytoplankton is not usually expressed as a ratio of dry mass, and as the amount of phytoplankton eaten is comparatively small (see later), it was assumed that only a small error would be introduced by applying the carbon content value for zooplankton to the entire food intake. The total annual carbon intake by anchovy was estimated to be 260 000 t and 625 000 t for the West and South Coasts respectively. The annual consumption, in terms of dry mass, was 6,9 times the mean standing stock of anchovy.

Species composition of the diet of anchovy

The results given here are derived from those presented by James (1987), and are expressed as the percentage contribution of phytoplankton, micro-zooplankton (20-200u), meso-zooplankton (200-2000u) and macro-zooplankton (>2000u) to the total carbon content of the diet. The contribution of these components to the diet was estimated from the reconstructed (undigested) masses of the items in the stomachs, as described by James (op. cit.). Tables V-VIII give the percentage compositions of the stomach contents averaged over trawl samples taken during November 1983 (South Coast) and May 1983, April 1984 and May 1984 (West Coast), for anchovy >80 mm and $\leq$ 80 mm Lc. Also given are the standard deviations and ranges of the individual station values (the station values were means for

Table V. Diet composition (% carbon) of anchovy sampled over the Agulhas Bank off the South Coast during November 1983. (n = number of trawl stations sampled.)

	Lc > 80 mm (n = 33)			Lc ≤ 80 mm		
Diet component	Mean	SD	range	Mean	SD	range
Phytoplankton	1,1	1,8	0 - 6,1			
Micro-zooplankton	2,7	5,5	0 -19,0			
Meso-zooplankton	61,2	38,0	1,4-99,7			
Macro-zooplankton	34,9	39,4	0 -98,6			

Table VI. Diet composition of anchovy sampled off the West Coast during May 1983. (n - number of trawl stations sampled.)

	Lc > 80 mm (n = 14)			Lc ≤ 80 mm (n = 17)		
Diet component	Mean	SD	range	Mean	SD	range
Phytoplankton	38,6	33,7	0 -90,1	32,2	39,3	0 -96,1
Micro-zooplankton	2,0	5,1	0 -19,2	2,9	5,3	0 -16,4
Meso-zooplankton	29,3	33,1	0,7-99,1	39,2	32,9	3,7-100,0
Macro-zooplankton	30,1	40,3	0 -99,0	25,7	34,6	0 -96,0

Table VII. Diet composition (% carbon) of anchovy sampled off the West Coast in May 1984. (n = number of trawl stations sampled.)

	Lc > 80 mm (n = 10)			Lc ≤ 80 mm (n = 14)		
Diet component	Mean	SD	range	Mean	SD	range
Phytoplankton	0,8	1,8	0 - 5,0	1,3	3,3	0 - 4,9
Micro-zooplankton	9,0	19,6	0 -55,5	1,0	3,1	0 -28,0
Meso-zooplankton	9,5	15,6	0,4-42,7	13,1	26,2	0,2-79,9
Macro-zooplankton	80,7	36,2	4,8-99,8	84,5	31,8	5,2-99,8

Table VIII. Diet composition (% carbon) of anchovy sampled off the West Coast during April 1984. (n - number of trawl stations sampled.)

	Lc > 80 mm (n = 11)			Lc ≤ 80 mm (n = 14)		
Diet component	Mean	SD	range	Mean	SD	range
Phytoplankton	3,1	2,4	0,4-8,0	13,9	17,2	0,1-55,9
Micro-zooplankton	6,1	11,3	0,3-36,6	11,1	17,3	0,6-64,7
Meso-zooplankton	79,2	23,7	31,5-95,6	73,0	26,1	27,8-94,9
Macro-zooplankton	11,6	23,2	0 -67,0	1,9	5,6	0 -21,3

samples of up to 50 fish). The data for the West Coast are summarized in Table IX for all sizes of anchovy combined, and the arithmetic means of the estimates from the three West Coast surveys are also given.

The data in Tables V-VIII show great variation in the composition of the stomach contents between stations. The fish sampled off the South Coast during November 1983 had been feeding predominantly on meso- and macro-zooplankton, the phytoplankton component attaining a maximum of 6,1%. The contribution of phytoplankton to the stomach contents of fish sampled off the West Coast ranged from 1% to 35% between surveys, and was more than 90% at some stations in May 1983. Although E. capensis is considered to be primarily zoophagous, juveniles schooling near upwelling sites within 10-40 miles of the West Coast are more likely to encounter densities of phytoplankton that are high enough to elicit filter feeding than would be the case over much of the offshore Agulhas Bank.

Estimates of the annual consumption of different size-categories of plankton by anchovy are given in Table X. The diet of pre-recruit anchovy was assumed to be made up entirely of micro- and meso-zooplankton in the same relative proportions as recorded for older anchovy off the West Coast. These results show that South African anchovy feed mainly on meso- and macro-zooplankton. The predominance of phytoplankton in the diet of adult anchovy sampled

Table IX: Summary of data on diet of anchovy sampled off the West Coast in different surveys, with both size ranges combined. Standard errors for the estimates in each year are given in parenthesis. The arithmetic means are given.

	Survey			
Diet component	May 1983	May 1984	April 1984	Mean
Phytoplankton	35,06 (6,55)	1,12 (0,56)	9,18 (2,78)	15,12
Micro-zoopl.	2,53 (0,93)	4,35 (2,67)	8,91 (2,97)	5,26
Meso-zoopl.	34,72 (5,90)	11,62 (4,50)	75,73 (4,95)	40,69
Macro-zoopl.	27,69 (6,59)	82,91 (6,73)	6,18 (3,26)	38,93

Table X: Estimates of the annual consumption by anchovy, in thousand tons of carbon, of different size categories of plankton

Diet component	Pre-recruits: West Coast	Post-recruits: West Coast	Post-recruits: South Coast
Phytoplankton		35,0	6,9
Micro-zooplankton	3,2	12,2	16,9
Meso-zooplankton	24,8	94,3	382,9
Macro-zooplankton		90,2	218,4
Total	28,0	231,7	625,1

off Namibia by King and Macleod (1976) probably reflects an extreme case of the prey selectivity model proposed for anchovy by James (1987).

ABUNDANCE AND DIET OF OTHER MIDWATER AND PELAGIC PLANKTIVORES

Estimates of abundance

PILCHARD

Estimates of the abundance of pilchard are available from acoustic surveys in November 1984-1989, August 1986 and February 1987 (Table XI, Armstrong et al. in prep). These estimates are subject to an unknown bias related to the estimate of target strength, which was obtained from a report on in situ. target strength experiments on the clupeids herring and capelin (Halldorsson and Reynisson 1983). The estimates of biomass showed an increase of an order of magnitude between 1984 and 1989, and supporting evidence for a substantial increase of this nature is provided by data on egg abundance and the occurrence of pilchard in the diet of predators (Armstrong et al. op. cit.). The dynamics of the population are poorly understood, and it is not possible to reconstruct cohorts with acceptable accuracy. Estimates of biomass for the West and South Coasts are given in Table XI, and the averages over the period 1984-1988 are shown. Where two estimates were available in one year, these were averaged prior

Table XI: Estimates of biomass of pilchard (in thousands of tons) obtained by echo-integration during the years 1984-1989. The West Coast includes the region from Cape Point to St Helena Bay or the Orange River in different years (data from Armstrong et al. in prep.). Regions: SHB - St Helena Bay; OR - Orange River; HB - Hondeklip Bay; CC - Cape Columbine

Survey	Most northerly region surveyed	West Coast	(CV)	South Coast	(CV)
Nov. 1984	SHB	0	-	32	(0,87)
Nov. 1985	CC	0	-	54	(0,39)
Aug. 1986	-	-	-	260	(0,30)
Nov. 1986	SHB	14	(1,0)	140	(0,46)
Feb. 1987	OR	97	(0,32)	216	(0,51)
Nov. 1987	HB	79	(0,55)	48	(0,48)
Nov. 1988	HB	38	(0,60)	79	(0,87)
Nov. 1989	CC	89	(0,73)	266	(0,20)
Mean: 1984-1988		47	(0,6)	99	(0,5)

to obtaining a mean of the annual estimates.

ROUND HERRING

Estimates of the biomass of round herring were obtained from acoustic surveys in August 1986, February 1987 and November 1989 (Table XII, Payne and Armstrong in prep.). A comparatively stable biomass in the region of 1,0-1,5 million tons is indicated. The same expression for target strength that was applied to acoustic data on pilchard and anchovy was utilized and hence the biomass estimates are subject to bias of an unknown magnitude. Only one survey (February 1987) adequately covered the West Coast region to the north of Cape Columbine, but only extended to 50 nautical miles offshore in most of this region. Payne and Armstrong (in prep.) present distribution maps derived from bottom-trawl surveys that show a widespread distribution of adult round herring over the West Coast shelf, extending out to some 500 m sounding. Hence, the estimates of biomass of round herring off the West Coast shown in Table XII must be regarded as highly inaccurate. As with pilchard, the dynamics of the round herring population are poorly understood, and reconstructions of cohorts have not been attempted.

MESOPELAGIC FISH

The sternoptychid Maurolicus muelleri (lightfish) and the myctophid Lampanyctodes hectoris (lanternfish) are widespread and abundant members of the neritic fish community over the West

Table XII: Estimates of biomass of round herring (in thousands of tons) obtained by echo-integration during the years 1986-1989. Key for regions as in Table XI. Data from Payne and Armstrong (in prep.)

Survey	Most northerly region surveyed	West Coast	(CV)	South Coast	(CV)
Aug. 1986	-	-	-	1062	(0,16)
Feb. 1987	OR	196	(0,43)	1377	(0,17)
Nov. 1989	CC	121*	(0,70)	909	(0,21)

* Known underestimate

Coast shelf (Hulley and Prosch 1987, Armstrong and Prosch in press). The abundance of lightfish was estimated by Armstrong and Prosch (op. cit.) from acoustic data collected during February 1987, and from monthly egg abundance data collected during the years 1977 and 1978. Their estimates of mean fish density were in the range 4,0 to 10,0 tons.km^{-2}, giving biomasses of 0,5 to 1,2 million tons for a habitat area of some 120 000 km^2. From data on egg abundances obtained during the pelagic acoustic cruises in November 1983-1988, Armstrong and Prosch (op. cit.) showed that with the exception of the year 1986, when few lightfish eggs were present, the mean density of eggs was relatively constant over this period. Hence, for the purposes of the present paper, it has been assumed that the biomass of lightfish during the years 1984-1988 was in the range 0,5-1,2 million tons (mean 0,85 million tons).

The biomass of lanternfish in the southern Benguela is essentially unknown. However, Armstrong and Prosch (in press) give data on the species composition of 48 midwater trawl catches of lightfish and lanternfish taken during the years 1987, 1988 and 1989 that indicate an approximately equal abundance of the two species on average. Hence, the average biomass of lanternfish over the period 1984-1988 has also been assumed to be in the range 0,5-1,2 million tons.

Rates of food consumption of species other than anchovy

Although Wallace-Fincham (1987) showed diel patterns of stomach fullness of round herring that were similar to the patterns of stomach mass in anchovy presented earlier, insufficient data were available to model the diel pattern of stomach content mass and hence to estimate the daily food consumption rates of species other than anchovy. It has been assumed that the daily consumption rate in these species is similar to that of anchovy, although a considerable range of uncertainty must be allowed.

Species composition of the diet

Applicable studies on the diet of the pelagic species under consideration here are those of Davies (1957) on pilchard, Wallace-Fincham (1987) on round herring, and the review on the diet of clupeoids by James (1988). The latter author indicated that the most striking features of most investigations of the diet of clupeoids are the great variability in species composition within and between studies, and the unreliability of straightforward analyses of gut contents as a method of determining trophic habits. Davies (op. cit.) estimated that two-thirds of the diet of pilchard comprised phytoplankton, the remaining third comprising zooplankton. He utilized a method of analysis that combined counting of the food items and a visual assessment of the relative volumes of the items. However, Cushing (1978) reviewed this study and stated that the importance of zooplankton would have appeared greater had a proper volumetric analysis taken place. It can be

inferred from the data in Davies' (1957) paper that some 90% of the zooplankton component of the diet comprised copepods. Davies' samples came primarily from the West Coast, where upwelling causes dense blooms of diatoms, whereas during the 1980s, the population of pilchards was distributed predominantly over the Agulhas Bank. As is the case with anchovy, it is likely that zooplankton are a more important component of the diet of pilchard off the South Coast than off the West Coast, because of the comparatively low production of diatoms over the Agulhas Bank. However, during an acoustic survey in November 1989, pilchards had accumulated over the inner shelf where upwelling at Capes along the South Coast had resulted in cool water containing blooms of diatoms (Armstrong et al. in prep.). This illustrates the potentially large variability in distribution and diet of a highly mobile fish such as pilchard, and the degree of error that could be introduced to analyses of material flow through the food web by drawing on the results of stomach-content analyses that have been based on limited sampling over space and time.

Wallace-Fincham's (1987) analyses of round-herring stomachs showed this species to be zoophagous, as expected for a particulate feeder. She does not summarize her findings in terms of micro-, meso- or macro-zooplankton. However, for round herring longer than 11cm sampled over the Agulhas Bank in November 1983 and 1984 (Wallace-Fincham 1987, her Tables 5 and 6), euphausiids, mysids and amphipods comprised 40% of the diet by mass, the remaining 60%

being predominantly copepods. Wallace-Fincham (op. cit.) does not give data for 11cm+ fish off the West Coast, and it is assumed that the diet in this region is similar to that off the South Coast.

Diet studies on South African lanternfish are very limited, and do not exist for lightfish. Prosch (1986) reviews the data that are available that indicate an approximately equal contribution of meso- and macro-zooplankton to the diet of lanternfish sampled from the South African purse-seine catches. Other studies on feeding of myctophids have shown a similar split between meso- and macro-zooplankton, with a tendency towards a predominance of macro-zooplankton (Hopkins and Baird 1985, Tyler and Pearcy 1975, Sameoto 1988). On the basis of these findings, it has been assumed that on average the ratio of meso- to macro-zooplankton in the diet of lanternfish is 40:60. The same ratio has been adopted by Hewitson and Cruickshank (this volume) for estimating the food intake of lanternfish off Namibia. It is assumed that the diet of lightfish is similar to that of lanternfish. This assumption is also based on crude observations by one of the authors (MJA) of the stomach contents of lightfish collected during an acoustic survey in November 1989.

The inferences on composition of the diet of pilchard, round herring, lanternfish and lightfish are summarized in Table XIII. The confidence ranges are arbitrary and are not based on statistical estimates of precision, and are given for the testing of the

sensitivity of network analyses utilizing this information on diet.

ANNUAL CONSUMPTION OF FOOD BY PELAGIC AND MESOPELAGIC FISH

Table XIV gives estimates of the most likely annual levels of food consumption by pilchard, round herring, lightfish and lanternfish off the West and South Coasts, in addition to the estimates for anchovy, and ignoring at this stage the levels of error associated with these estimates. The estimate of total annual consumption of carbon by the pelagic fish assemblage off the West Coast is 1944 000 t, and almost double this at 3520 thousand tons off the South Coast. Some 95% of this intake is comprised of meso- and macro-zooplankton.

Sources of error in estimates of annual consumption of food

Table XV summarizes the successive steps involved in estimating the annual consumption of phytoplankton, micro-, meso-and macro-zooplankton by the five species of planktivorous fish considered here, and an indication is given if the information is based on actual estimates or on assumptions. From Table XV it is clearly

Table XIII: Percentage composition of the diet of pilchard, round herring, lightfish and lanternfish, as inferred from published and unpublished sources of data (see text). Figures in parenthesis are guesses of the likely confidence ranges of the estimates, for testing the sensitivity of network analyses utilizing this information

Species	% Phytoplankton	% Meso zooplankton	% Macro zooplankton
Pilchard	67 (34-83)	30 (15-60)	3 (2-6)
Round herring	0	60 (30-80)	40 (20-70)
Lanternfish	0	40 (20-70)	60 (30-80)
Lightfish	0	40 (20-70)	60 (30-80)

Table XIV: Estimates of the annual consumption of food (in thousands of tons of carbon) by pilchard, round herring, lightfish and lanternfish off South Africa, assuming the same daily rate of food intake as estimated for anchovy. Figures for anchovy are also given

(a) West Coast

Species	Annual food consumption (t. carbon.10^{-3})					
	Biomass (t.10^{-3})	Phyto plankton	Micro-zoopl.	Meso-zoopl.	Macro-zoopl.	Total
Anchovy	300	35	15	119	90	259
Pilchard	47	27		12	1	40
Round herring	200			104	69	173
Lightfish	850			294	441	735
Lanternfish	850			294	441	735
Total	2247	62	15	823	1 042	1 942

(b) South Coast

Species	Annual food consumption (t. carbon.10^{-3})					
	Biomass (t.10^{-3})	Phyto plankton	Micro-zoopl.	Meso-zoopl.	Macro-zoopl.	Total
Anchovy	723	7	17	383	218	625
Pilchard	99	58		26	3	87
Round herring	1 000			519	346	865
Total	1 822	65	17	928	567	1 576

Total West + South	4 069	127	32	1 751	1 609	3 519

Table XV: Sources of error in estimates of annual food consumption by pelagic fish, at each step in the calculation. EA - estimated from analysis of field data with relatively small systematic errors expected; EB - estimated from analysis of field data with unquantified biases present; ? - assumed by comparison with other species. The last column gives the form and magnitude of errors assumed for investigation of overall variance in estimates of annual consumption

Estimation step	Anch.	Pil.	R.herr.	Light fish	Lantern fish	Error distribution
Estimation of biomass	EA	EB	EB	EB	?	Lognormal; log SD=0,35
Conversion to dry mass	EA	?	?	?	?	Uniform; range = 0,25-0,35
Estimation of daily food intake	EA	?	?	?	?	Lognormal; log SD=0,35
Conversion from dry mass to carbon	EA	EA	EA	EA	EA	Uniform; range = 0,36-0,48
Species composition of diet	EA	EB	EB	?	EB	Multinomial (see text)

apparent that there are very large gaps in understanding of the biomass, food consumption rate and diet of the most abundant species such as mesopelagic fish and round herring. In most cases the errors are unquantifiable because assumptions with unknown biases have had to be invoked. Hence it has not been possible to provide realistic estimates of variance for the estimates of annual consumption of different size-categories of plankton.

However, by making assumptions on the form and magnitude of error distributions, it is possible to illustrate potential levels of variance resulting from errors in the different parameters and variables from which the annual rates of consumption are derived. The assumptions with regard to errors are summarized in Table XV. The error distributions associated with conversion to dry-mass or to carbon were specified as being uniform with ranges inferred from information given by James (1987) or from unpublished data. Error distributions for biomass and daily food intake were specified as being log-normal with log standard deviations of 0,35. This represents a 95% range of half to double the median value. In the case of the species composition of the diet, the error distributions will be multi-nomial. For the present exercise, only the consumption of meso-zooplankton was considered, and the error distribution around the proportion in the diet comprising meso-zooplankton (g) was assumed log-normal for values of g less than 0,5, with a log standard deviation of 0,35 (approximating the ranges given in Table XIII). Where the value of g was greater than

0,5, a log-normal distribution of (1-$\underline{q}$) was generated (i.e. to create an error distribution of $\underline{q}$ skewed to the right).

By selecting randomly from the different error distributions, a set of 3000 realizations of the data was generated for the West Coast and the South Coast, and the 3000 values of annual food intake were compiled into a probability distribution (Fig. 6). In the case of log-normal distributions, the median was first calculated from the mean value before generating a random variable:

$$\underline{B}' = \underline{B} * \exp(-o^2/2) * \exp(\ ) \qquad (4)$$

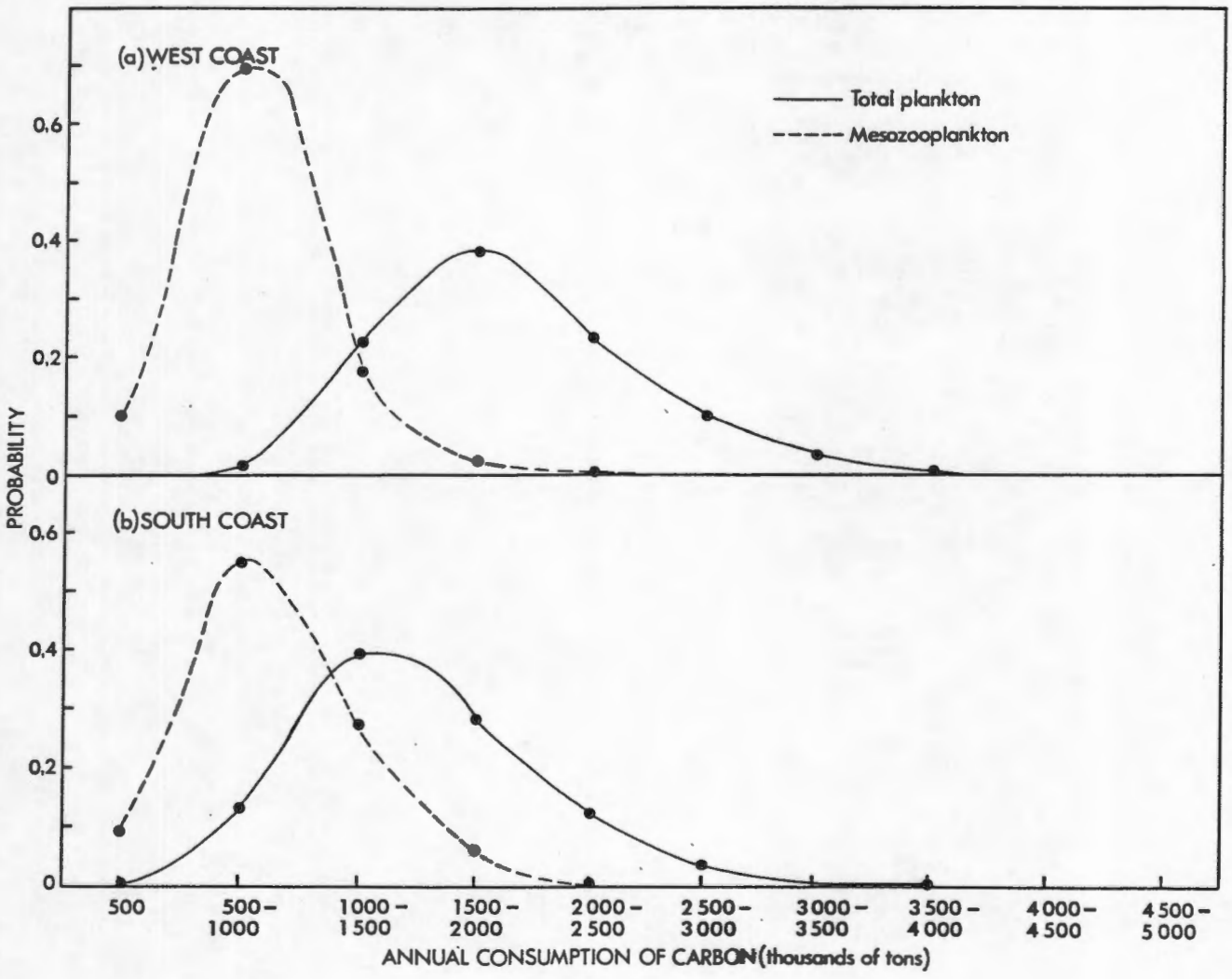
where $\underline{B}'$ is a random value of (in this case) biomass that would be utilized in one realization of the data set;

o is the standard deviation of the logarithmic error distribution; and

is a random variable drawn from a normal distribution with mean of zero and standard deviation of o.

The log-normal error distributions were truncated at $\pm$ 3 standard deviations, and values of $\underline{q}$ less than 0,01 or greater than 0,99 were rejected. The resultant error distributions around total annual food intake and total annual intake of meso-zooplankton indicate the considerable uncertainty surrounding these estimates. For example, 95% confidence limits on total consumption of carbon by the pelagic and mesopelagic fish assemblage off the West Coast

Fig. 6. Error distributions for estimates of total annual consumption of carbon by anchovy off the West and South Coasts, representing the contribution of plausible levels of error in estimates of biomass, daily food intake and factors for converting from wet to dry mass and from dry mass to mass of carbon (see Table XV). Also shown are error distributions for estimates of annual consumption of meso-zooplankton.



are conservatively estimated to be of the order of 1-3 million tons.

CONCLUSIONS

Earlier estimates of the consumption of food by planktivorous fish in the southern Benguela system were based on highly biased estimates of biomass obtained by means of Virtual Population Analysis of data from commercial catches, over-optimistic estimates of daily consumption rates, and figures for species composition of the diets that over-emphasized the contribution of phytoplankton. For example, Shannon and Field (1985) estimated the total annual consumption of carbon for a total biomass of pelagic fish of 0,8 million tons from the mid 1960s, but assuming daily consumption rates of 6-12% body mass per day (wet mass ratios). These figures represent a probable under-estimate of biomass by a factor of five (arising from errors associated with VPA and exclusion of mesopelagic fish), and an over-estimate of daily consumption by more than a factor of two. Hence the estimate of total annual food consumption of 1,7 million tons of carbon given by Shannon and Field (op. cit.) is about half the estimate of 3,5 million tons given in the present study (Table XIV). The estimate of total annual consumption of phytoplankton given by Shannon and Field (op. cit.) is based on a 67% contribution of this food item to the diet of pelagic fish, whereas the present study shows that off the West

and South Coasts, the consumption of phytoplankton by the pelagic and mesopelagic fish assemblage during the 1980s has probably been less than 5% of the total carbon intake (Table XIV).

The principal finding of the present study is that an assemblage of some 4 million tons (wet mass) of pelagic and mesopelagic fish occurring over the continental shelf of South Africa may have an annual consumption of approximately 3,5 million tons of carbon, over 90% of which is likely to be derived from meso- and macrozooplankton eaten in roughly equal proportions. Certain aspects of these findings need to be emphasized:

1) Unquantified and potentially large biases and variances are associated with estimates of biomass, distribution, daily food intake and diet composition of abundant mid-shelf species such as round herring, lightfish and lanternfish;

2) Seasonal patterns in the variables mentioned in (1) may have a strong influence on the annual food intake, but are very poorly understood at present;

3) Averages made over large areas and time-scales may be misleading in a network analysis of material flow, for example because of the patchy aggregations typical of pelagic fish and the large inter-annual variations in abundance that can occur.

An intensive study of the West Coast or South Coast ecosystem, involving successive surveys over a year to investigate biomass, distribution, food consumption levels and diet of planktivorous fish, would be necessary to establish adequately the trophic dynamics of this component of the system. Such a study would allow the identification of key variables and processes that should be monitored to investigate the longer-term dynamics of the ecosystem and to facilitate interpretation of those time-series of data.

LITERATURE CITED

ARMSTRONG, M.J., SHELTON, P.A., HAMPTON, I., JOLLY, G. and Y.C. MELO 1988 - Egg production estimates of anchovy biomass in the southern Benguela system. *Rep. Calif. coop. oceanic Fish. Invest.* 29: 137-157.

ARMSTRONG, M.J. and R.M. PROSCH (in press) - Abundance and distribution of the mesopelagic fish *Maurolicus muelleri* in the southern Benguela system. *S. Afr. J. mar. Sci.*

ARMSTRONG, M.J., HAMPTON, I., ROEL, B.A., VALDES, E.S. and J. VAN DER WESTHUIZEN (in prep) - The recent increase in abundance of pilchard *Sardinops ocellatus* off South Africa.

BADENHORST, A. and A.J. BOYD 1980 - Distributional ecology of the larvae and juveniles of the anchovy *Engraulis capensis* Gilchrist in relation to the hydrological environment off South West Africa, 1978/79. *Fish. Bull. S. Afr.* 13: 83-106.

BERGH, M.O., FIELD, J.G. and L.V. SHANNON 1985 - A preliminary carbon budget of the southern Benguela pelagic ecosystem. In *International Symposium on the Most Important Upwelling Areas off Western Africa (Cape Blanco and Benguela)[,Barcelona, 1983]* 1. Bas, C., Margalef, R. and P. Rubies (Eds). Barcelona; Instituto de Investigaciones Pesqueras: 281-304.

BERGH, M.O. and D.S. BUTTERWORTH 1987 - Towards rational harvesting of the South African anchovy considering survey imprecision and recruitment variability. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 937-951.

COCHRANE, K. (this volume) - Biomass and primary production: system interactions.

CRAWFORD, R.J.M. 1981 - Distribution, availability and movements of anchovy *Engraulis capensis* off South Africa, 1964 - 1976. *Fish. Bull. S. Afr.* 14: 51-94.

CUSHING, D.H. 1978 - Upper trophic levels in upwelling areas. In *Upwelling Ecosystems*. Boje, R. and M. Tomczak (Eds). New York; Springer: 101-110.

DAVIES, D.H. 1957 - The South African pilchard (*Sardinops ocellata*). Preliminary report on feeding off the West Coast, 1953-56. *Investl Rep. Div. Fish. S. Afr.* 30: 40 pp.

HALLODRSSON, O. and P. REYNISSON 1983 - Target strength measurements of herring and capelin *in situ* at Iceland. In *Symposium on Fisheries Acoustics. Selected Papers of the ICES/FAO Symposium on Fisheries Acoustics, Bergen, Norway, June 1982.* Nakken, O. and S.C. Venema (Eds). *F.A.O. Fish. Rep.* 300: 78-84.

HAMPTON, I. 1987 - Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 901-917.

HAMPTON, I. and M.J. ARMSTRONG (in prep) - Migration patterns of anchovy *engraulis capensis* off South Africa deduced from acoustic surveys.

HUGGET, J. and S. PAINTING (in prep) - Zooplankton biomass and egg production in relation to anchovy recruits.

HUTCHINGS, L. and W. PETERSON (in prep) - Chlorophyll, particle spectra, zooplankton biomass and production in relation to hydrography and anchovy spawners.

HEWITSON, J.D. and R.A. CRUICKSHANK (this volume) - The role of pelagic fish in the northern Benguela ecosystem.

HOPKINS, T.L. and R.C. BAIRD 1985 - Aspects of the trophic ecology of the mesopelagic fish *Lampanyctus alatus* (Family Myctophidae) in the eastern Gulf of Mexico. *Biol. Oceanogr.* 3(3): 285-313.

HULLEY, P.A. and R.M. PROSCH 1987 - Mesopelagic fish derivatives

in the southern Benguela upwelling region. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 597-611.

JAMES, A.G. 1987 - Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 673-692.

JAMES, A.G. 1988 - Are clupeid microphagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. *S. Afr. J. mar. Sci.* 7: 161-177.

JAMES, A.G. and K.P. FINDLAY 1989 - Effect of particle size and concentration on feeding behaviour, selectivity and rates of food ingestion by the Cape anchovy *Engraulis capensis*. *Mar. Ecol. Prog. Ser.* 50: 275-294.

JAMES, A.G., PROBYN, T. and L.J. SEIDERER 1989 - Nitrogen excretion and absorption efficiencies of the Cape anchovy *Engraulis capensis* Gilchrist fed upon a variety of plankton diets. *J. Exp. Mar. Biol. Ecol.* 131: 101-124.

JARRE, A., PALOMARES, M.L., SORIANO, M.L., SAMBILAY JR.,V.C. and D. PAULY (in press) - Some improved analytical and comparative

methods for estimating the food consumption of fishes. *Proceedings of the ICES Symposium on Multispecies Management*, 1989.

KING, D.P.F. and P.R. MACLEOD 1976 - Comparison of the food and the filtering mechanism of pilchard *Sardinops ocellata* and anchovy *Engraulis capensis* off South West Africa, 1971-1972. *Investl Rep. Sea Fish. Brch S. Afr.* **111**: 29 pp.

KJELSON, M.A., PETERS, D.S., THAYER, G.W. and G.N. JOHNSON 1975 - The general feeding ecology of post larval fishes in the Newport River Estuary. *Fish. Bull. NOAA* **73**: 137-144.

LASKER, R. 1985 - What limits clupeoid production? *Can. J. Fish. aquat. Sci.* **42**(Suppl. 1): 31-38.

PROSCH, R.M. 1986 - Early growth in length of the anchovy *Engraulis capensis* Gilchrist off South Africa. *S. Afr. J. mar. Sci.* **4**: 181-191.

PROSCH, R.M. 1986 - The biology, distribution and ecology of *Lampanyctodes hectoris* and *Maurolicus muelleri* along the South-African coast. M.Sc. thesis; University of Cape Town: viii + 197 pp.

SAMEOTO, D.D. 1988 - Feeding of lanternfish *Benthosema glaciale* off

the Nova Scotia shelf. *Mar. Ecol. Prog. Ser.* **44**: 113-129.

SHANNON, L.V. and J.G. FIELD 1985 - Are fish stocks food-limited in the southern Benguela pelagic ecosystem? *Mar. Ecol. Prog. Ser.* **22**(1): 7-19.

SHELTON, P.A. 1986 - Fish spawning strategies in the variable southern Benguela Current region. Ph.D. thesis, University of Cape Town: [vi] + 327 pp.

SHELTON, P.A., BOYD, A.J. and M.J. ARMSTRONG 1985 - The influence of large-scale environmental processes on neritic fish populations in the Benguela Current system. *Rep. Calif. coop. oceanic Fish. Invest.* **26**: 72-92.

SWART, V.P. and J.L. LARGIER 1987 - Thermal structure of Agulhas Bank water. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 243-253.

TYLER, H.R. and W.G. PEARCY 1975 - The feeding habits of three species of lanternfishes (Family Myctophidae) off Oregon, USA. *Mar. Biol.* **32**(1): 7-11.

VALDES, E.S., SHELTON, P.A., ARMSTRONG, M.J. and J.G. FIELD 1987 - Cannibalism in South African anchovy: egg mortality and egg

consumption rates. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 613-622.

VERHEYE, H.M. and L. HUTCHINGS 1988 - Horizontal and vertical distribution of zooplankton biomass in the southern Benguela, May 1983. *S. Afr. J. mar. Sci.* 6: 255-265.

WALDRON, M., ARMSTRONG, M.J. and R.M. PROSCH 1989 - Aspects of the variability in growth of juvenile anchovy *Engraulis capensis* in the southern Benguela system. *S. Afr. J. mar. Sci.* 8: 9-19.

WALDRON, M., ARMSTRONG, M.J. and B.A. ROEL (in prep) - Birthdate distributions of the 1985 and 1989 year-classes of anchovy *Engraulis capensis* deduced from acoustic and midwater trawling surveys and daily growth analysis.

WALLACE-FINCHAM, B.P. 1987 - The food and feeding of *Etrumeus whiteheadi* Wongratana 1983, off the Cape Province of South Africa. M.Sc. thesis, University of Cape Town: 117 pp.

CHAPTER 4

THE ENERGETICS AND EVOLUTION OF INTRASPECIFIC PREDATION (EGG CANNIBALISM) IN THE ANCHOVY, *Engraulis capensis*

Edy Valdes

Sea Fisheries Research Institute, Private Bag X2, 8012 Rogge Bay, South Africa

Key words: *Engraulis capensis*, intraspecific predation, energetics, anchovy, South Africa.

ABSTRACT

Anchovy feeding activity peaks twice daily, a minor peak between 07h00 and 09h00 and a more pronounced one between 17h00 and 19h00. Mean daily consumption in the field was estimated at 3.75% of body weight per day. Since the various food types available to anchovy differ in their caloric values this figure might be expected to vary according to the type of diet available to the fish. To obtain a diet energetically equivalent to that measured in the field anchovy feeding exclusively on phytoplankton would need to consume the equivalent of 5.8% of their body weight per day and those feeding on zooplankton 3.5 - 4.5% of the body weight, while fish feeding on their own eggs would require only 2.5% of their body weight daily. Feeding on eggs at peak spawning on the spawning grounds -where there is limited alternative food (i.e. zooplankton) available- seems adequate to support reproduction. The thermodynamic implication of egg consumption as an energy regulating mechanism at a time of great energy expenditure is to maintain calories within a population but at the expense of negative entropy. This, decreases the ecological efficiency of secondary production and poses difficulties for an operational

concept of a trophic level. In selection at the population level, cannibalistic fish benefit from homeostatic self-regulation.

I. INTRODUCTION

During peak spawning each female Cape anchovy *Engraulis capensis*, generally spawns a new batch of eggs every 12 days (Chapter 1). Batch fecundity did not change significantly between 1986 and 1988, and nor did the spawning fraction at peak spawning (Chapter 1). Hunter and Leong (1981) concluded that feeding conditions (at least during the first months of spawning) may not greatly affect batch fecundity in northern anchovy *Engraulis mordax*, but it may well influence the frequency of spawning. Before the decline of the Pacific sardine *Sardinops sagax*, most northern anchovy spawned only in the winter quarter, instead of in spring and summer quarters, which are the normal periods for sardine spawning. After the decline in sardine, anchovy larval production in winter and spring was about equal. The increased duration of the peak period of spawning of northern anchovy was interpreted by Hunter and Leong (1981) as the result of food being made available by the collapse of the Pacific sardine. This additional food was used by the northern anchovy to increase the number of spawning batches produced annually.

Northern anchovy consume mainly zooplankton (Loukashkin, 1970), whereas the Peruvian anchovy *Engraulis ringens* feeds on a mixed ration of phytoplankton and zooplankton, with a preference for one or the other according to where the fish live, in the north

or south of the Peruvian ecosystem respectively (Rojas de Mendiola, 1971). Cape anchovy consume mainly phytoplankton and eggs in their spawning grounds on the western Agulhas Bank at peak spawning (Valdes, unpublished data), but for the rest of the year zooplankton dominates their diet (James, 1987).

Because anchovy are highly opportunistics foragers (Koslow, 1981; Angelescu, 1982; James, 1987), their diet may be a direct reflection of the availability of food resources. Different spawning fractions in the Benguela system, off California and off Peru (Chapter 1) may therefore be explained in terms of the different rates of cannibalism on anchovy eggs following from the different availability of food to them in the three ecosystems. Energy regulation of fecundity by availability of food may well be important as a density-dependent regulation mechanism, as shown for other fish by Bagenal (1973).

Peterson and Hutchings (1989), on the basis of the results of a combined acoustic/spawning fraction research cruise along the south and west coasts of South Africa in Nov/Dec 1988, stated that anchovy spawners on the western Agulhas Bank were supported by the local production of zooplankton. Their results showed that secondary production in the anchovy spawning area on the western Aguhlas Bank between Cape Point and Cape Agulhas was low. Concentrations of fish in the area were high, but the concentrations of small phytoplankton and zooplankton were low. The water was a warm 18-19°C and the thermocline was moderately deep at 30-40 m. Peterson and Hutchings emphasized that inshore upwelling

resulted in high concentrations of large phytoplankton within 10-20 km of the shore, but still very low levels of zooplankton. Their conclusion was that, over the western Bank, the fish could not be sustained by local production.

Valdes *et al.* (1987) found that cannibalism on anchovy eggs may account for 70% of the total egg mortality for one area of high density of eggs on the western Agulhas Bank. This intraspecific mechanism seemed to the authors to be density-dependent, regulating egg survival as a predictable function of egg density. Of course, egg density is greater immediately after spawning because of dispersal of older eggs and, at such a time, cannibalism may be more intense. Furthermore, because spawning starts at about 18h00 and peaks at about 21h00 (Armstrong *et al.* 1988), more or less coincident with peak feeding (see below), the abundance and the high density of eggs at that time will most probably elicit anchovy feeding on their own progeny (MacCall, 1981). Brownell (1985) reported on larval cannibalism by *E. capensis* in laboratory experiments and suggested that under nutritional limitations and in presence of a sufficiently wide distribution of fish size, cannibalism was indeed a population regulatory mechanism.

To evaluate the anchovy energy budget at spawning and the importance of various food types in supporting this budget, a knowledge of the caloric equivalents of the different food particles is required. The objectives of this study were:
1) Based on Chapter 3, to discuss the feeding periodicity of Cape

anchovy (*Engraulis capensis*) and its relation to availability of prey.

2) To evaluate the caloric values of different food items and to consider their availability at the peak spawning grounds.

3) To assess the energetic consequences of intraspecific predation and its implication for natural selection.

II. MATERIALS AND METHODS

Anchovy samples were collected in November 1986, 1987 and 1988 during surveys designed mainly to estimate the spawner biomass of the species (Hampton, 1987). The survey design is given in Chapter 2.

Fish were blast-frozen immediately after capture. In the laboratory they were dissected. Length, weight, maturation stage, gonad and stomach content weights, time of capture and station position were recorded routinely for every sample of 25 fish from each trawl sample. Stomach contents were preserved in 4% formaldehyde solution for later examination.

To estimate the daily feeding periodicity of anchovy, the ratio of the mean wet weight of stomach contents to the wet weight of fish as a percentage (the fullness index as suggested by Hureau, 1969; but given as wet instead of dry weight) per trawl was plotted for the data at two-hour intervals during each of the three years (as also is shown in somewhat similar manner in Chapter 3).

To obtain caloric values, anchovy eggs (hydrated oocytes) from hydrated females were dried for 24 h at 60°C and dessicated in a silica-gel dessicator to constant weight. They were then made into pellets for combustion. Similar analyses were carried out with a mixture of different species of phytoplankton from laboratory cultures (*Pavlova lutheri*, *Chaetoceros didymus*, *Chaetoceros gracilis* and *Thalassiosira weissflogii*). All combustion was done in a Parr 1241 automatic, adiabatic calorimeter adapted for a microbomb. Combustion samples for each food item were carried out in triplicate according to standard techniques.

III. RESULTS

1. Diel feeding cycle

The diel feeding pattern of anchovy, shown in a somewhat different manner from that in Chapter 3, is given in Figure 1. There was a period of low feeding intensity extending from about 02h00 to 09h00, peaking between 07h00 and 09h00, and a period of intense feeding which extends from about 13h00 to 19h00, peaking between 17h00 and 19h00. The daily ration of Cape anchovy was -on average- 3.75% of fish wet weight per day (Chapter 3).

2. Energy budget

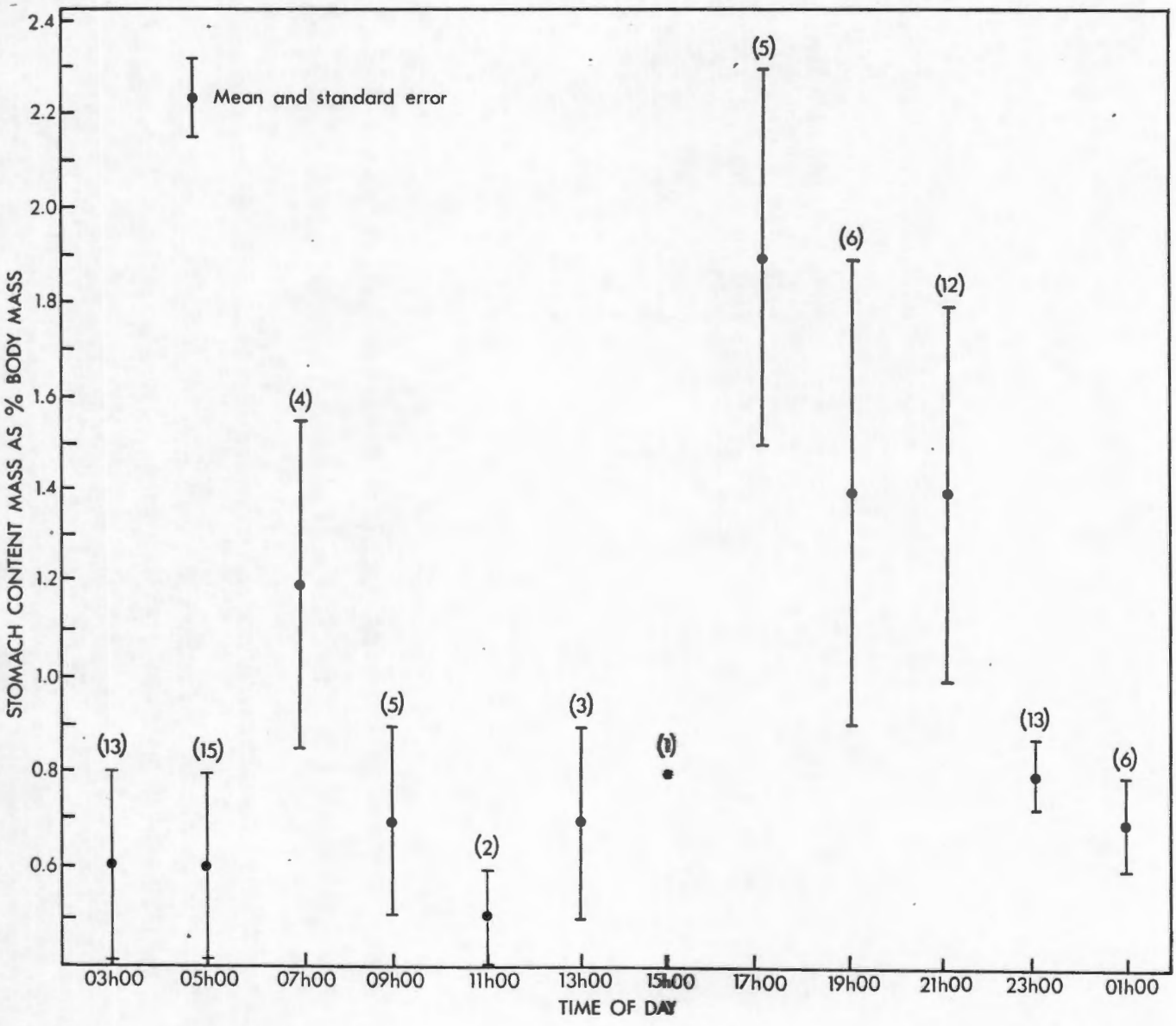
An estimate of the hypothetical energy requirements and equivalent rations of different food items that need to be eaten by Cape anchovy can be made from the data of Hunter and Leong

(1981) on the energetic daily ration for northern anchovy. In the present paper the caloric value of phytoplankton and anchovy eggs (hydrated oocytes) and their water content were estimated. Laurence (1976) estimated the caloric value of different species of calanoid copepods.

For a given daily ration of 1.4 kJ d^{-1} for an anchovy of 10.3 g (Hunter and Leong, 1981), considering the 26.8 kJ g^{-1} dry weight for *Calanus finmarchicus* (Laurence, 1976), and adjusting this value to wet weight by the average water content of *Calanus* (84.7% - Lovegrove, 1966), a ration of *Calanus finmarchicus* of about 3.5% of the body wet weight per day is calculated to be equivalent to a caloric intake of 1.4 kJ d^{-1}.

The same procedure was used to calculate the caloric value of the diet of a fish feeding on a calanoid copepod (i.e. *Temora longicornis* - Laurence, 1976) with a lower caloric value. This species has a significantly lower energetic value than *Calanus finmarchicus* (18.7 kJ g^{-1} dry weight). A fish would need to consume about 4.5% of its wet body weight per day to obtain an equivalent caloric ration of 1.4 kJ d^{-1}. Therefore, these two different copepods may account for a ration from 3.5-4.5% of the fish wet weight.

Fig. 1 Feeding periodicity of *E. capensis*. Points are means for 25 fish per sample taken from several trawls at 2 h intervals. The number of trawls is indicated in parenthesis.



A similar calculation may be made for anchovy feeding on their own eggs, if it is assumed that the caloric value of hydrated oocytes can be applied to unfertilized eggs or the first embryonic stages of fertilized eggs. The average caloric value of eggs is 23.8 kJ g^{-1} dry weight (SD= $\pm$ 0.8). Adjusting this value to wet weight by allowing for the estimated average water content (76.6%) gives a caloric equivalent of 5.6 kJ g^{-1} wet weight. On this basis an anchovy could meet its energy requirements by consuming about 2.5% of its wet weight per day in its own eggs.

If anchovy feed exclusively on phytoplankton, which has a caloric value of 15.5 kJ g^{-1} dry weight (SD= $\pm$ 1.2) and an estimated percentage of water of 84.3%, then 5.8% of the wet body weight needs to be consumed daily to provide the same ration of 1.4 kJ d^{-1}.

IV. DISCUSSION

1. Feeding periodicity, daily ration and intraspecific predation

Figure 1 shows that anchovy have two preferred feeding periods, but that the rate of consumption is greater in the second, which

peaks from about 17h00 to 19h00. The major peak in feeding activity was also found by Valdes *et al.* (1987) in a specific area of the Agulhas Bank and by James (1987) during his studies on clupeoid feeding on the west coast of South Africa. The larger set of data used in Chapter 3 allowed the identification of the second, smaller early-morning feeding peak (Fig. 1).

For the Peruvian anchovy, Jarre *et al.* (1989), on the basis of data presented by Rojas de Mendiola (1989) and/or Alamo (1989), found that feeding peaked at midnight, not very different timing from feeding of the Cape anchovy. However, Peruvian anchovy apparently have just one daily preferred feeding period (Jarre *et al.* 1989), in contrast to two for the Cape anchovy. Nevertheless, Rojas de Mendiola (1981), for the same Peruvian anchovy, reported that, based on the condition of the food in the stomach in relation to the time of the catch, anchovy probably feed in the morning around 09h00, again between 18h00 and 20h00 and finally around midnight. However, the last two periods may reflect the feeding period reported by Jarre *et al.* (1989). It may well be that because anchovy are caught mainly at night, Jarre *et al.* (1989) did not use sufficient data for day-time to detect the peak at 09h00 mentioned by Rojas de Mendiola (1981).

Therefore, if this were the case, the findings on Cape anchovy feeding periodicity would be similar to those for Peruvian anchovy, except for a shift of 2-4 h in both daily feeding periods.

Jarre *et al.* (1989) also found that Peruvian anchovy consume an average daily ration of 3.0% of their body weight, similar to the value found for Cape anchovy. Hunter and Leong (1981) estimated a slightly higher average daily consumption of 4-5% body weight for northern anchovy. However, that higher figure may be the result of using a steady-state situation to estimate daily consumption, rather than the more dynamic approach used by Jarre *et al.* (1989) or in Chapter 3 of this thesis.

Nevertheless, different values for the percentages of body mass consumed may arise as a result of different diets. Anchovy, like any other living organism, must consume a daily ration which provides sufficient molecules of carbohydrate, fat and protein to obtain the necessary energy to maintain concentration gradients of ions to carry out biosynthetic reactions, to transport and secrete molecules across cell membranes, and to provide power for cell movement and muscle activity (Datta and Ottaway, 1970). Within certain limits (the maximum stomach volume), anchovy -as any other animal- can adjust the volume consumed daily according to their energetic requirements for sustaining metabolic activities (Gerking, 1978).

Egg production per female during the peak spawning season did not change from 1986 to 1988, although the number of spawnings during the year may have varied (Chapter 1). Because egg production per female depends partially on the quantity of food ingested at the time of the spawning (Hunter and Leong, 1981), it is concluded that availability of food to individual fish at the time of spawning would have been more or less constant if egg production per female was unchanged over the three years. Furthermore, spawning takes place more or less when feeding peaks (i.e. starting at 18h00, as reported by Armstrong *et al.* 1988), supporting a feedback between feeding and spawning. Therefore, rates of egg cannibalism in the Benguela may also be indicative of the availability of alternative food particles.

Cape anchovy have a complex feeding pattern in which adults mainly consume zooplankton (calanoid copepods), by raptorial feeding, as well as phytoplankton, mainly by filter-feeding (James, 1987). James postulated that anchovy filter-feed on particles <0.5 mm maximum dimension and selectively feed raptorially on items > 0.7 mm maximum dimension. Particles between 0.5 and 0.7 mm fall into a "grey area", in which predator size interacts with prey size and concentration to modify feeding behaviour.

Anchovy eggs measure approximately 1.34 mm by 0.66 mm, and therefore can be consumed by either filtration or biting. However, all observations of anchovy eggs in anchovy stomachs seem to correlate with the presence of phytoplankton and the

absence of zooplankton. Hence, it is assumed that anchovy eggs are consumed by filtering, a suggestion also made by Hunter and Kimbrell (1980) and MacCall (1981). The extent to which eggs are filtered selectively or taken inadvertently while filtering other prey is not known. Nevertheless, high densities of eggs occasionally recorded at peak spawning may be sufficient to cause the school to filter intensively within an aggregation of eggs.

On the western part of the Agulhas Bank, where most spawning of anchovy takes place (Armstrong *et al.* 1988), the abundance of zooplankton seems to be low (Peterson and Hutchings, 1989). There is, however, a good density of phytoplankton and, of course, anchovy eggs. Hence, filter-feeding would seem likely to be the dominant feeding pattern and there is most probably a selective feeding on eggs, driven by the energetic richness of this food and its relative abundance, at least in some places.

Monitoring the daily ration as a percentage of body mass does not adequately reflect differences in diet. Diet would be best estimated by calculating energetic consumption rather than the volume or mass eaten. Not only is the caloric value of food important, but also its composition. The food consumed must ensure an adequate intake of the necessary proteins, lipids and carbohydrates, plus minerals and vitamins.

A daily ration of 3.75% of wet body weight was necessary during November of 1986, 1987 and 1988 to support the spawning fish (Chapter 3). As phytoplankton cells and anchovy eggs are the most

abundant particles of the appropriate size available to be consumed by filter-feeding anchovy when they are spawning, and given their respective energy value it can thus be speculated that a mixed diet of both provide the necessary 3.75% of body wet weight per day.

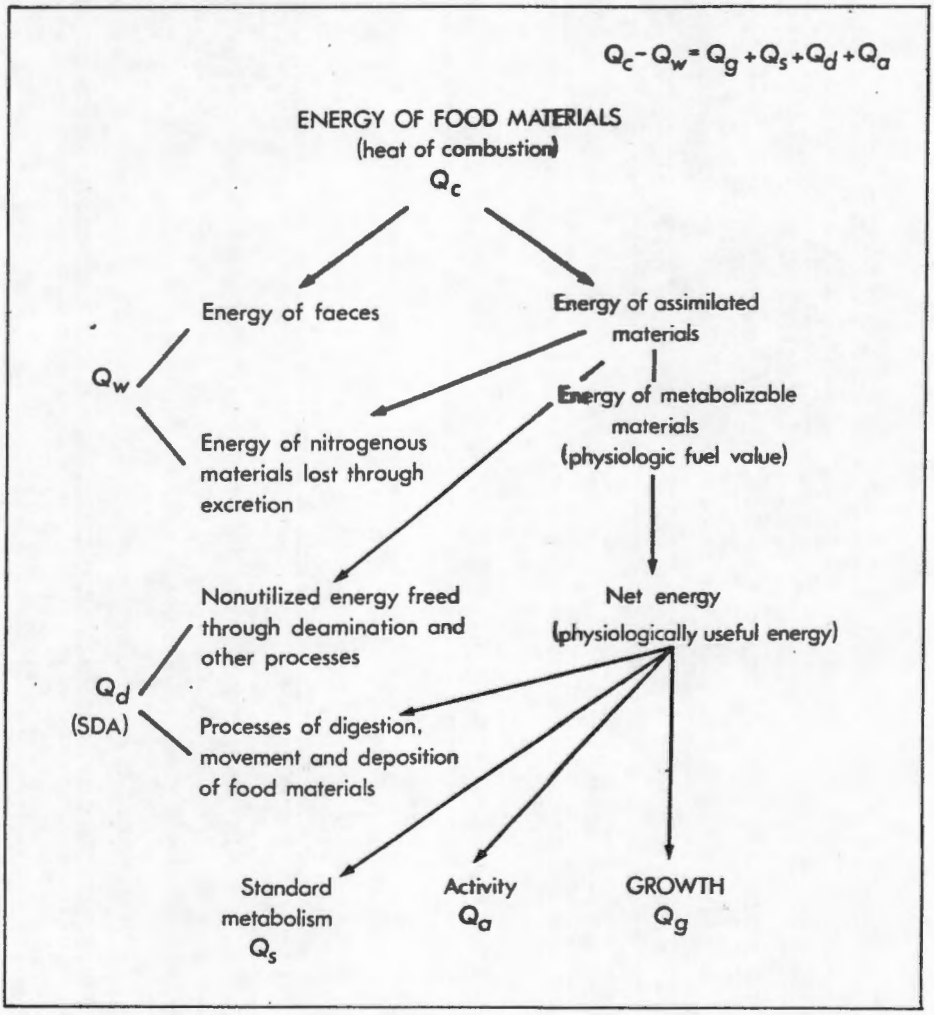
In addition, anchovy require an important supply of proteins from their food at spawning, because energy expenditure then is high. Although phytoplankton are made up (by dry weight) of 40-55% of protein, 20-40% of carbohydrate and some 20-25% of lipid (Ketchum and Redfield, 1949), the proportion of carbohydrates (polysaccharides: starch and leucosin) and lipid (polyunsaturated fatty acids) to protein (Boney, 1975) is relatively higher than in fish eggs or zooplankton. Therefore, a mixed ration with eggs would more efficiently provide the energy and proteins necessary for spawning. Eggs are richer in proteins than phytoplankton. They are particularly rich in yolk proteins, which are mainly lipovitellin (glycolipophosphoproteins) with a very low content of alkali-labile phosphorus. Some species also have phosvitin (rich in phosphorus but lacking in lipid and carbohydrate) in their eggs (Hoar, Randall and Donaldson, 1983). The energetic value estimated here for anchovy eggs (i.e. 23.8 kJ g^{-1} dry weight) was not significantly different ($P < 0.05$) from the value estimated by Hunter and Leong (1981) for the northern anchovy (22.8 kJ g^{-1} dry weight).

Energetic content and food composition is not sufficient to characterize a food good for fish. It is also necessary that the

chemical bonds correspond with the metabolic capacity of the predator so that the bonds can easily be broken down and the full caloric content assimilated (Margalef, 1980). In that sense, the chitin of copepods (the main zooplankton taxa consumed by Cape anchovy; James, 1988) contains less nourishment than is suggested by its energetic value (Margalef, 1980). Phytoplankton organisms also have cell walls composed of cellulose, silicon dioxide or alginic acid, etc. (Dawes, 1981), all of which are also less nutritional than suggested by their energetic value (Margalef, 1980). On the contrary, the digestibility of anchovy eggs (and therefore its capacity for assimilation; Fig. 2) is much higher to anchovy than are either zooplankton or phytoplankton.

When predators consume at their own trophic level, the efficiency of such intake is greater than the average energy transfer between one trophic level and the next (Margalef, 1980), but it is at the expense of negative entropy (Giese, 1968). Their high capacity for assimilating anchovy eggs is probably the reason why Hunter and Kimbrell (1980) estimated such a fast rate of gastric evacuation for such food consumed by northern anchovy. Even if zooplankton was not so scarce on the anchovy spawning grounds, it may be concluded that, although zooplankton organisms are as rich in protein as eggs (zooplankton has only 5-10% fat and 12-20% carbohydrates; Wickstead, 1976), their digestibility is certainly lower.

Fig. 2 Losses and uses of consumed food materials (after Warren and Davis, 1967).



O'Connell (1972) suggested that filtering provides a continuous intake of food for *Engraulis mordax*, with biting supplying the remainder of the daily ration. James and Probyn (1989) argue that such a method is energetically uneconomic for the Cape anchovy because of the high energy output required to sustain filtering when compared to that required for normal swimming (James and Findlay, 1989). Bearing these arguments in mind, it is quite conceivable that Cape anchovy might consume some eggs by raptorial feeding, depending on their density, rather than by filtering, as the size of eggs determines whether they can be ingested either by filtration or raptorially (James, 1987). If the concentration of eggs is high enough, it may be energetically more advantageous for the fish to feed raptorially because is less expensive and provides a higher return (James and Probyn, 1989).

If a much smaller ration of eggs than phytoplankton or zooplankton needs to be consumed in order to obtain the necessary energy for each fish, and if such consumption requires less effort than feeding exclusively on phytoplankton, then eating eggs in the spawning season (when zooplankton is scarce) may be advantageous to survival and to the maintenance of a certain spawning frequency (Hunter and Leong, 1980).

2. Energetics and population regulation

Bearing in mind that there is no evidence of interannual

variation in the anchovy egg production per female at the peak spawning season from 1986 to 1988 (Chapter 1), the significance of anchovy egg cannibalism and its implication as an energy-regulatory mechanism at a time of great energy expenditure (i.e. spawning time) leads to the question of what is the energetic value of consuming eggs in order to spawn them?

Hunter and Leong's (1981) data in Table 1 indicate that dry weight of *E. mordax* declines by about 30% during the main spawning season as a result of loss of fat. This loss is equal to the energy required for some 13 spawnings. Therefore, the loss of energy per batch spawned would be about 2.3% of dry body weight. From Hunter and Leong's Table 4 plus an assumption that dry body weight equals 25% of wet weight, an estimate of the cost per spawning of about 4.4% of body weight for an average female can be obtained (Clarke, 1986).

Hunter and Leong (1981) noted that about two-thirds of the annual cost of egg production can be accounted for by the annual decline in fat stores. In other words, anchovy accumulate fat during the year to support spawning, but the protein for egg production must come from food intake during the spawning season. Even if the same statement holds true for Cape anchovy, the additional requirements for continued spawning would have to come from the food assimilated and available for reproduction over a period of 12 days (Chapter 1) rather than 8 days for *E. mordax* (Bindman, 1986). Assuming the cost per batch to be 4% of the dry body weight and that 65% of this comes from body reserves in both

E.mordax. and *E. capensis*, the average additional requirements per day would be 0.2% (Clarke, 1986) and 0.1% body weight respectively.

Theoretically, reproductive effort can be modulated by changes in batch fecundity, annual number of spawnings, egg size, female size at first maturity and egg cannibalism. The first two of these were discussed in Chapter 1, where no interannual variation in egg production per female of Cape anchovy at peak spawning season could be detected, although the number of spawnings during the year may have varied. Alheit and Alegre (1986) and Alheit (1989) reach similar conclusions regarding no interannual variability in batch fecundity of the anchovy in Peru and California respectively. In terms of size at first maturity, there is no evidence that female Cape anchovy vary in size at first maturity. As for egg cannibalism Valdes (1986) suggests that, in the Cape anchovy this may be a potentially very important compensatory mechanism of stock size and could be the reflection of the availability of food resources. In Chapter 2, a model was proposed to estimate anchovy recruitment based on egg data, in which intra-specific and interspecific density-dependent mechanisms (suggested to be mainly egg cannibalism and sardine predation on anchovy eggs respectively) are the factors responsible for regulating effective egg production and thus, egg survival to recruitment, because intensity of cannibalism and predation can change with population size.

Thermodynamically, anchovies, like any other living organisms,

during periods of ecological stress (i.e. severe water stratification which may lead to poor primary and secondary production), or in areas of poor secondary production, such as over the western Agulhas Bank. Egg cannibalism may be inherently different from cannibalism on older individuals, but they both reduce the numbers of potential competitors that would have shared resources as the fish grew older (Fox, 1975). Cannibalism may be in part an adaptation that, by increasing food availability and reducing potential competition, promotes greater fitness in more cannibalistic than in less cannibalistic conspecifics.

At the population level, cannibalistic fish benefit from homeostatic self-regulation. The anchovy populations may be self-regulated below the carrying capacity of the environment, increasing its stability. At low levels of food availability, cannibalism may contribute to continued reproduction and, thus, to continued survival of the population at a certain level. However, it is clear that cannibalism is not perfectly homeostatic under all demographic and environmental conditions. Under certain conditions (i.e. high local density but low overall abundance of eggs) it may cause the depletion or loss of an entire age-class. Nevertheless, in normal situations, density-dependent rates of mortality are compensatory for stock size.

If food is limiting for pelagic fish in the Benguela ecosystem, as suggested by Shannon and Field (1985), a feedback loop between

intraspecific predation and ambient food occurs (Polis, 1981): 1) As conspecifics are eaten, the population of intraspecific competitors declines and the *per capita* food level increases. 2) As fish is satiated by cannibalism, there is a decrease in feeding (effectively increasing *per capita* food).

ACKNOWLEDGEMENTS

I would like to formally and sincerely thank Drs. K. Cochrane and A. Payne (Sea Fisheries Research Institute) and Professor Raul Vaz Ferreira (Universidad de la Republica, Montevideo) who have read early versions of this manuscript and provided valuable criticisms. Letters exchanged with Professor G. Polis (Vanderbilt University, Tennessee) and reading his papers provided new ides and clarification of my thoughts on the dynamics and evolution of cannibalism and intraguild predation. Dr. J. Alheit (Polarmar, Bremerhaven) has constantly sent to me articles and references which provided a host of insights and made me learn about the mechanisms of fecundity and cannibalism in the anchovy. I am especially indebted to my supervisor, Professor C. Griffiths (University of Cape Town) for generous and cheerful help to improve the contents and style by carefully reviews of the various drafts of this manuscript. I also thank the technical staff of the Sea Fisheries Research Institute for assistance in the collection of the data during sea cruises. Mr.C. Boothroyd,

Mr. J. Van der Westhuizen and Mr. F. Kriel are particularly thanked for help in processing the data and for the calorimetric analyses. Mr. A.P. van Dalsen and his staff were responsible for the artwork. This work is being submitted in partial fulfilment of the requirements of Ph.D. at the University of Cape Town.

REFERENCES

ALAMO, A. 1989 - Stomach contents of anchoveta (*Engraulis ringens*), 1974-1982. In *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*. Pauly, D., Muck, P., Mendo, J. and B. Rojas de Mendiola (Eds). ICLARM Conference Proceedings 18: 105-108.

ALHEIT, J. 1989 - Comparative spawning biology of anchovies, sardines and sprats. *Rapp. P-v. Reun. Cons. int. Explor. Mer.* **191**: 7-14.

ALHEIT, J. and B. ALEGRE 1986 - Fecundity of Peruvian anchovy, *Engraulis ringens*. *ICES Working Document* **CM 1986/H:60**: 12 pp.

ARMSTRONG, M.J., BUTTERWORTH, D.S., HAMPTON, I., PAYNE, B.A., PUNT, A. and P.A. SHELTON (in preparation) - Survey-based management of the multi-species pelagic clupeoid fishery of the southern Benguela upwelling system.

ARMSTRONG, M.J., SHELTON, P.A. HAMPTON, I., JOLLY, G. and Y.C. MELO 1988 - Egg production estimates of anchovy biomass in the southern Benguela system. *Rep. Calif. coop. oceanic Fish. Invest.* **29**: 137-157.

BAGENAL, T.B. 1973 - Fish fecundity and its relations with stock and recruitment. *Rapp P-v. Reun. Cons. int. Explor. Mer.* **164**: 186-198.

BINDMAN, A.G. 1986 - The 1985 spawning biomass of the northern anchovy. *Rep. Calif. Coop. Oceanic Fish. Invest.* **27**: 16-24.

BONEY, A.D. 1975 - Phytoplankton. Edward Arnold, London, 116 pp.

BROWNELL, C.L. 1985 - Laboratory analysis of cannibalism by larvae of the Cape anchovy *Engraulis capensis*. *Trans. Am. Fish. Soc.* **114**(4): 512-518.

CLARKE, T.A. 1986 - Fecundity and spawning frequency of the Hawaiian anchovy or nehu, *Encrasicholina purpurea*. *Fishery Bull., Wash.* **85** (1): 127-138.

DATTA, S.P. and J. H. OTTAWAY 1970 - *Bioquimica*. Paidos, Buenos Aires, 436 pp.

DAWES, C.J. 1981 - *Marine botany*. John Wiley & Sons, New York, 628 pp.

FOX, L.R. 1975 - Cannibalism in natural populations. *A. Rev. of Ecol. Syst.* 6: 87-106

GERKING, S. D. 1978 - *Ecology of freshwater fish production*. Blackwell, London, 520 pp.

GIESE, A.C. 1968 - *Fisiologia General*. Interamericana, Mexico, 603 pp.

HAMPTON, I. 1987 - Acoustic study on the abundance and distribution of anchovy spawners and recruits in South African waters. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 901-917.

HOAR, W.S., RANDALL, D.J. and E.M. DONALDSON 1983 - *Fish physiology*. Academic Press, New York, 483 pp.

HUNTER, J.R. and C.A. KIMBRELL 1980 - Egg cannibalism in the northern anchovy, *Engraulis mordax*. *Fishery Bull., Wash.* 78(3): 811-816.

HUNTER, J.R. and R.J.H. LEONG 1981 - The spawning energetics of female northern anchovy, *Engraulis mordax*. *Fishery Bull., Wash.* 79(2): 215-230.

HUREAU, J.C. 1969 - Biologie comparee de quelques poissons antarctiques (Nototheniidae). *Bull. Inst. Oceanogr. Monaco* 68(1391): 244 pp.

JAMES, A.G. 1987 - Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 673-692.

JAMES, A.G. 1988 - Are clupeid microphagists herbivorous or

omnivorous? A review of the diets of some commercially important clupeids. *S. Afr. J. mar. Sci.* **7**: 161-177.

JAMES, A.G. and K.P. FINDLAY 1989 - Effect of particle size and concentration on feeding behaviour, selectivity and rates of food ingestion by the Cape anchovy *Engraulis capensis*. *Mar. Ecol. Prog. Ser.* **50**: 275-294.

JAMES, A.G. and T. A. PROBYN 1989 - The relationship between respiration rate, swimming speed and feeding behaviour in the Cape anchovy, *Engraulis capensis* Gilchrist. *J. Exp. Mar. Biol. Ecol.* **131**: 81-100.

JARRE, A. PALOMARES, M.L., SORIANO, M.L. SAMBILAY, V.C. and D. PAULY 1989 - Some improved analytical and comparative methods for estimating the food consumption of fishes. In *Proceedings of the ICES Symposium on Multispecies Models relevant to Management of Living Resources, Den Haag, Netherlands, October 1989* **Paper 12**: 19 pp.

KETCHUM, B.H. and A.C. REDFIELD 1949 - Some physical and chemical characteristics of algae growth in mass culture. *J. Cell. Comp. Physiol.* **33**: 281-299.

LAURENCE, G.C. 1976 - Caloric values of some North Atlantic calanoid copepods. *Fishery Bull.*, Wash. **74**: 218-220.

LOUKASHKIN, A.S. 1970 - On the diet and feeding behaviour of the

northern anchovy, *Engraulis mordax (Girard). Proc. Calif. Acad. Sci., Ser. 4* 37(13): 419-458.

LOVEGROVE, T. 1966 - The determination of the dry weight of plankton and the effect of various factors on the value obtained. In *Some Contemporary Studies in Marine Science.* Barnes, H. (Ed.). London; George Allen and Unwin: 429-467.

MacCALL, A.D. 1981 - The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis.* In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, 1980.* Sharp, G.D. (Conv. Ed.). Paris; Unesco: 201-220 (*I.O.C. Workshop Rep.* 28).

MARGALEF, R. 1980 - *Ecologia.* Omega, Barcelona, 951 pp.

O'CONNELL, C.P. 1972 - The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax). J. Fish. Res. Bd Can.* 29: 285-293.

PETERSON, W.T. and L. HUTCHINGS 1989 - Chlorophyll, particle spectra, zooplankton biomass and production in relation to hydrography and anchovy spawners on the Agulhas Bank. Extended abstract. In *Proceedings of the Plankton Dynamics Mini-Symposium,* Cape Town, May 1989. *Rep. Benguela Ecol Progm. S. Afr.* 17: 81-95.

POLIS, G.A. 1981 - The evolution and dynamics of intraspecific predation. *A. Rev. Ecol. Syst.* 12: 225-251.

PRIGOGINE, I. 1955 - *Introduction to thermodynamics of irreversible processes.* Springfield, Illinois, 119 pp.

ROJAS de MENDIOLA, B. 1971 - Some observations on the feeding of the Peruvian anchoveta *Engraulis ringens* J. in two regions of the Peruvian coast. In *Fertility of the Sea.* Costlow, J. D. (Ed.). New York; Gordon and Breach: 417-440 (*Sci. Publ. 2).*

ROJAS de MENDIOLA, B. 1981 - Summary of the studies about food and feeding habits of the anchovy *(Engraulis ringens* J.). In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, 1980.* Sharp, G.D. (Conv. Ed.). Paris; Unesco: 221-231 (*I.O.C. Workshop Rep.* 28).

ROJAS de MENDIOLA, B. (in press) - Stomach contents of anchoveta *(Engraulis ringens)* 1953-1974. In *The Peruvian Upwelling Ecosystem: Dynamics and Interactions.* Pauly, D., Muck, P., Mendo, J. and I. Tsukayama (Eds). ICLARM Conference Proceedings.

SHANNON, L.V. and J.G. FIELD 1985 - Are fish stocks food-limited in the southern Benguela pelagic ecosystem? *Mar. Ecol. Prog. Ser.* 22(1): 7-19.

VALDES, E. 1986 - Egg Cannibalism by anchovy in the Southern Benguela Current region. M.Sc thesis. University of Cape Town: 85 pp.

VALDES, E.S., SHELTON, P.A., ARMSTRONG, M.J. and J.G. FIELD 1987 - Cannibalism in South African anchovy: egg mortality and egg consumption rates. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 613-622.

WARREN, C.E. and DAVIS, G.E. 1967 - Laboratory studies on the feeding, bioenergetics, and growth of fish. In *The Biological Basis of Freshwater Fish Production*. Gerking, S.D. (Ed.). Blackwell, Oxford 175-214 pp.

WICKSTEAD, J.H. 1976 - *Marine zooplankton*. Edward Arnold, London, 59 pp.

C H A P T E R 5

CANNIBALISM AND INTRAGUILD PREDATION IN CLUPEOIDS

Edy Valdes

Sea Fisheries Research Institute, Private Bag X2, 8012 Rogge Bay, South Africa

Key words: *Engraulis capensis*, *Sardinops ocellatus*, intraspecific predation, interspecific predation, anchovy, sardine, South Africa.

ABSTRACT

This paper provides empirical data to test hypotheses postulated in Chapter 2 of this thesis, where anchovy cannibalism and intraguild predation on anchovy by sardine were proposed to be compensatory mechanisms determining anchovy egg mortality and, hence, anchovy recruitment. The actual percentages of anchovy egg mortality caused by cannibalism and sardine predation are estimated herein. The rates of anchovy egg mortality during the period 1986-1988 averaged approximately 0.01 h^{-1}, representing a survival rate of about 55% over the 60-h incubation period. Some 56% of 3325 anchovy stomachs and some 88% of 1225 sardine stomachs in samples collected during the period 1986-1988 contained anchovy eggs. Of 750 sardines and anchovies caught in co-habited areas over the three years, 67% of the anchovy and 87% of the sardine had anchovy eggs in their stomachs. The mean numbers of eggs observed in stomachs per kilogramme of fish mass of the co-occurrent collections were 24 in anchovies and 2117 in sardines. An estimated up to 56% of the total anchovy egg mortality was the result of sardine predation and up to 6% was

the result of anchovy cannibalism. Fluctuations in anchovy recruitment and cycles in the abundance of clupeoid species in the Benguela system are likely attributable at least in part to these two mechanisms.

I. INTRODUCTION

A guild of planktivorous clupeoid species comprising the Cape anchovy (*Engraulis capensis*) and the South African pilchard or sardine (*Sardinops ocellatus)* is harvested by the South African purse-seine fishery. The two species combined yielded more than two million tons from 1984 to 1988. The fishery has been characterized by a "boom and bust" phenomenon of shifts in the distribution of both guild species over the years (Shannon *et al.* 1988), as has happened with similar clupeoid species in similar ecosystems around the world (Lasker and MacCall, 1983).

Species interactions involving predation are a major topic of discussion in fisheries. Predator-prey interdependence has been postulated as a possible cause of the appearance of "cycles" in abundance in guild species (Walters *et al.* 1986). Cannibalism has been proposed as a mechanism providing an upper limit to population density (Ricker, 1958; Hunter and Kimbrell, 1980; MacCall, 1981; Alheit, 1987; Valdes *et al.* 1987) of filter-feeding, pelagic-spawning, schooling coastal pelagic fish such as clupeoids. In other words, cannibalism can cause population self-regulation. On the other hand, predation by guild species may "regulate" the total biomass of competing species (Fox,

1975).

Population stabilization through compensating cannibalism is possible if predator abundance is constant and they have a sigmoid (type III) functional response to prey density (Holling, 1959; Murdoch, 1969; Peterman and Gatto, 1978). Increasing mortality may result if prey density increases and prey switching behaviour and/or numerical response increases (Murdoch, 1969; Murdoch *et al.* 1975).

In theory, density-dependent regulation might occur at any stage, including the egg (MacCall, 1981; Valdes *et al.* 1987). However, density-independent factors tend to mask the relatively weak density-dependent influences (MacCall, 1981; Welch, 1986).

If intraspecific predation occurs together with interspecific predation in the same guild, both may cause a synergistic effect reinforcing the possibility of long-term intraguild-predation-mediated shifts and the coexistence of sardine and anchovy in the Benguela system, as postulated in Chapter 2. In this open system, nonequilibrium behaviour (i.e. cyclical variations in the stock sizes of both species) may persist for long periods (Caswell, 1978).

In Chapter 2 it was postulated that the relative importance of intraguild predation by sardine or cannibalism by adult anchovy on their eggs might be the anchovy-recruitment-regulating response to clupeoid abundance, concentration and habitat

overlap. The purpose of this paper is therefore to provide empirical evidence on anchovy cannibalism and sardine predation and to show that rates of anchovy egg mortality may change as a result of the interaction of the guild species. Several parameters that may interact to determine the rate of intraspecific or interspecific predation on anchovy eggs from 1986 to 1988 will be considered in the present paper. They are:

1) The presence of anchovy eggs in the stomachs of the same and the other guild species (i.e. anchovy and sardine).

2) Variations in clupeoid abundance.

3) Variations in clupeoid concentration.

4) Spatial overlap between anchovy eggs and clupeoid predators.

5) Feeding periodicity and the availability of alternative prey items.

6) The functional relationship between egg density and egg consumption rate by individual fish (i.e. the functional response).

II. MATERIALS AND METHODS

Fish and plankton samples were collected off the South African coast during research cruises of the Sea Fisheries Research Institute's (SFRI) R.S. *Africana* in November 1986, 1987 and 1988. Survey design has been described and illustrated in Chapters 1 and 2, and therefore only a brief account is given here.

The investigation encompassed the spawning grounds of anchovy off South Africa on an intensive grid of plankton stations normally spaced 9.3 km apart. At each station anchovy eggs were sampled

by means of vertical hauls of a CalVET net (Smith *et al.* 1985) from 200 m deep or from as near the sea bed as possible. In areas of zero egg abundance, the distance between stations was frequently doubled (i.e. extended to 18.6 km).

1. Fish and plankton sampling and laboratory methods

Immediately after the completion of each tow, the plankton sample was preserved in 4-per-cent buffered formaldehyde in seawater. In the laboratory, anchovy eggs were removed from the plankton samples under a binocular dissecting microscope at 20 X magnification. Based on the degree of embryonic development and following the method of Moser and Alhstrom (1985), eggs were assigned to 11 stages, as described by Valdes *et al.* (1987). The abundance of each stage in the samples was standardized to the number under 1 m^2 of sea surface. The time of peak spawning was determined from the time of day at which newly fertilized eggs appeared in the egg collection and from observations of the occurrence of hydrated eggs in the ovaries of adult fish. The age of the eggs was determined to permit calculation of the rates of egg mortality and egg production. The methods used are fully described in Armstrong *et al.* (1988). Egg mortality and production estimates for 1986 used in this paper are taken from Armstrong *et al.* (1988), while those for 1987 and 1988 are taken from unpublished SFRI records.

Adult anchovy and sardine were caught by means of a midwater trawl, which was deployed if feasible immediately preceding or

following the CalVET net dip. Anchovy were caught in 60 and sardine in 47 of the midwater trawls taken in 1986, anchovy in 62 and sardine in 46 of the trawls in 1987, and anchovy in 41 and sardine in 28 of the 1988 trawls. For the present study a total of 182 trawl samples were analysed over the three years and 25 fish (either sardine or anchovy) were taken from each and blast-frozen immediately after capture (a total of 4550 fish, 3325 anchovy and 1225 sardine). In the laboratory, all fish were weighed and their stomachs removed. The number of anchovy eggs in each fish stomach was enumerated.

III. RESULTS

Of the 3325 anchovy analysed for presence and number of anchovy eggs in their stomachs, 950 were caught in 1986, 1550 in 1987 and 825 in 1988. On average 56% of the anchovy samples contained anchovy eggs. Of the 1225 sardine stomachs analysed (500 from 1986, 350 from 1987 and 375 from 1988), an average 88% contained anchovy eggs. Further, from the total number of trawl samples available for this study, only 14 trawls for 1986, 7 trawls for 1987 and 9 trawls for 1988 were found in which anchovy and sardine occurred together. In those samples, 67% of the anchovy and 87% of the sardine had anchovy eggs in their stomachs (Tables I, II and III).

The number of anchovy eggs found in anchovy stomachs during 1986, taken to be an index of cannibalism on their own eggs, is shown

in Fig. 1. The same figure also shows the anchovy egg distribution, monitored by plankton sampling, and the anchovy distribution, determined by acoustics and validated by midwater trawling. Fig. 2 contains similar data for the sardine. Both figures suggest that the degree of predation can be directly related to the degree of overlapping between the distributions of the fish and the eggs. There also seems to be an indication that, when the fish distribution overlaps the areas of greatest egg abundance, predation is the highest.

In Tables I, II and III, the numbers of anchovy eggs found per fish stomach in areas of co-occurrence of both species during 1986, 1987 and 1988 are summarized. In order to correct for the different sizes of anchovy and sardine and to compare the data of the two species on a weight to weight basis, the average number of eggs in the fish stomachs was calculated per kilogramme wet fish mass. For anchovy in 1986, each 1 kg of fish contained 18 anchovy eggs, but 1 kg of sardine contained two orders of magnitude more eggs (i.e. 1988 eggs) (Table I). During 1987, 1 kg of anchovy and sardine contained 58 and 549 anchovy eggs respectively (Table II), and in 1988, each kilogramme of anchovy and sardine contained 7 and 3189 anchovy eggs respectively in their stomachs.

The number of anchovy eggs consumed cannibalistically and by sardine predation was calculated according to the equation used by Hunter and Kimbrell (1980) for the northern anchovy *(Engraulis*

TABLE I: Mean number of anchovy eggs in stomachs per 1 Kg wet fish mass at trawl stations in november 1986 where sardine co-occurred with anchovy

Station (1986)	Anchovy	Sardine
01-03	0	16
06-05	22	21
07-03	62	294
11-01	3	109
14-01	0	53
14-05	23	131
15-06	89	525
23-05	15	0
27-12	10	105
30-07	0	1014
32-07	0	21
37-06	0	1655
38-07	0	5818
39-02	22	18069
Mean	17.6	1987.9

TABLE II Mean number of anchovy eggs in stomachs per 1 Kg wet fish mass at trawl stations in november 1987 where sardine co-occurred with anchovy

Station (1987)	Anchovy	Sardine
01-11	0	4
01-15	20	51
02-09	0	9
02-20	35	2670
04-14	0	0
16-01	5	1089
51-05	347	21
Mean	58.1	549.1

TABLE III Mean number of anchovy eggs in stomachs per 1 Kg wet fish mass at trawl stations in november 1988 where sardine co-occurred with anchovy

Station (1988)	Anchovy	Sardine
09-11	7	1473
09-13	1	6
19-07	0	3296
20-07	3	42
20-08	10	10909
21-06	31	7111
35-03	0	109
41-09	4	8896
43-09	10	0
Mean	6.6	3189.2

Fig. 1 Anchovy egg distribution monitored by CalVET net sampling, distribution of adult fish monitored by acoustics and the places where cannibalism occurred.

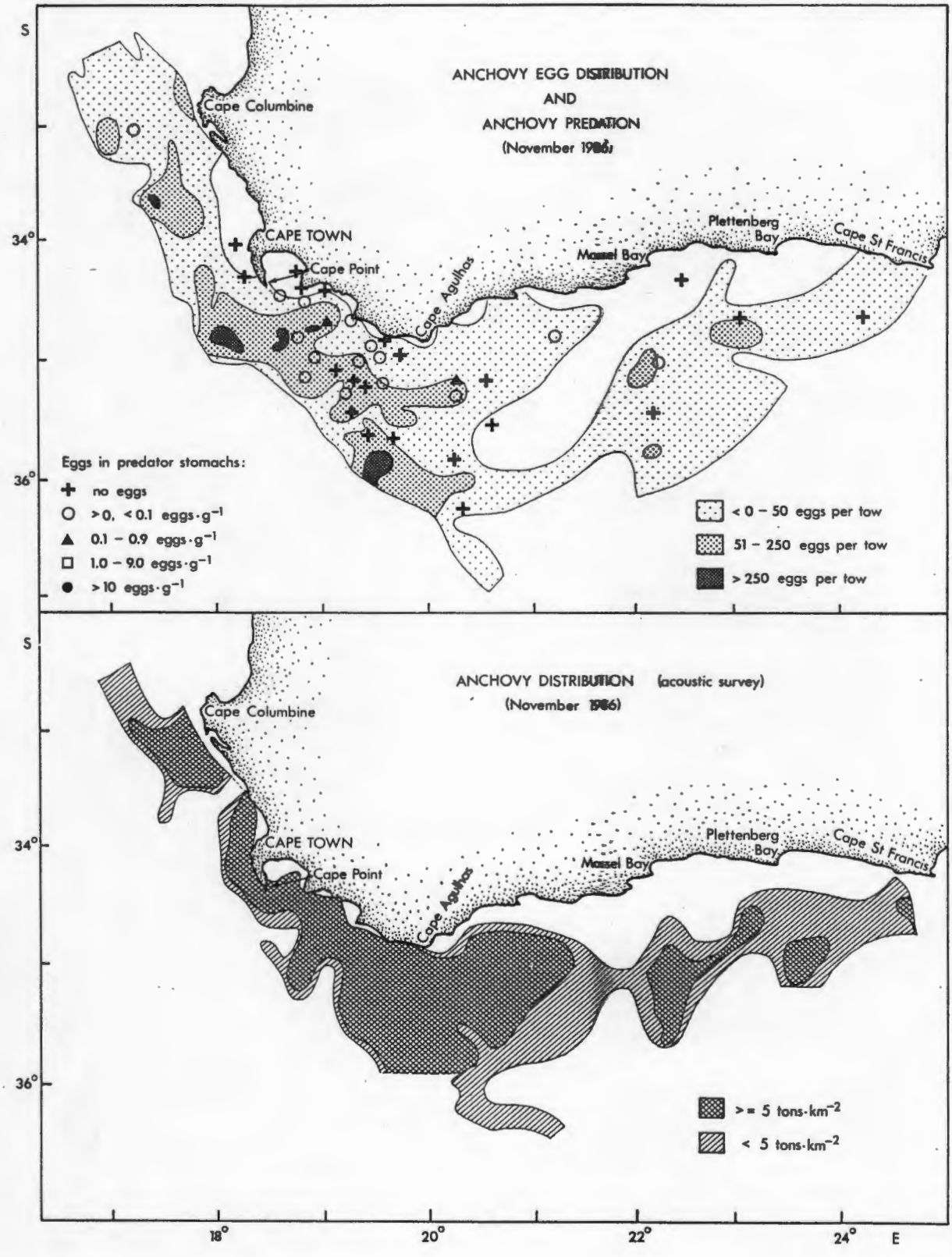
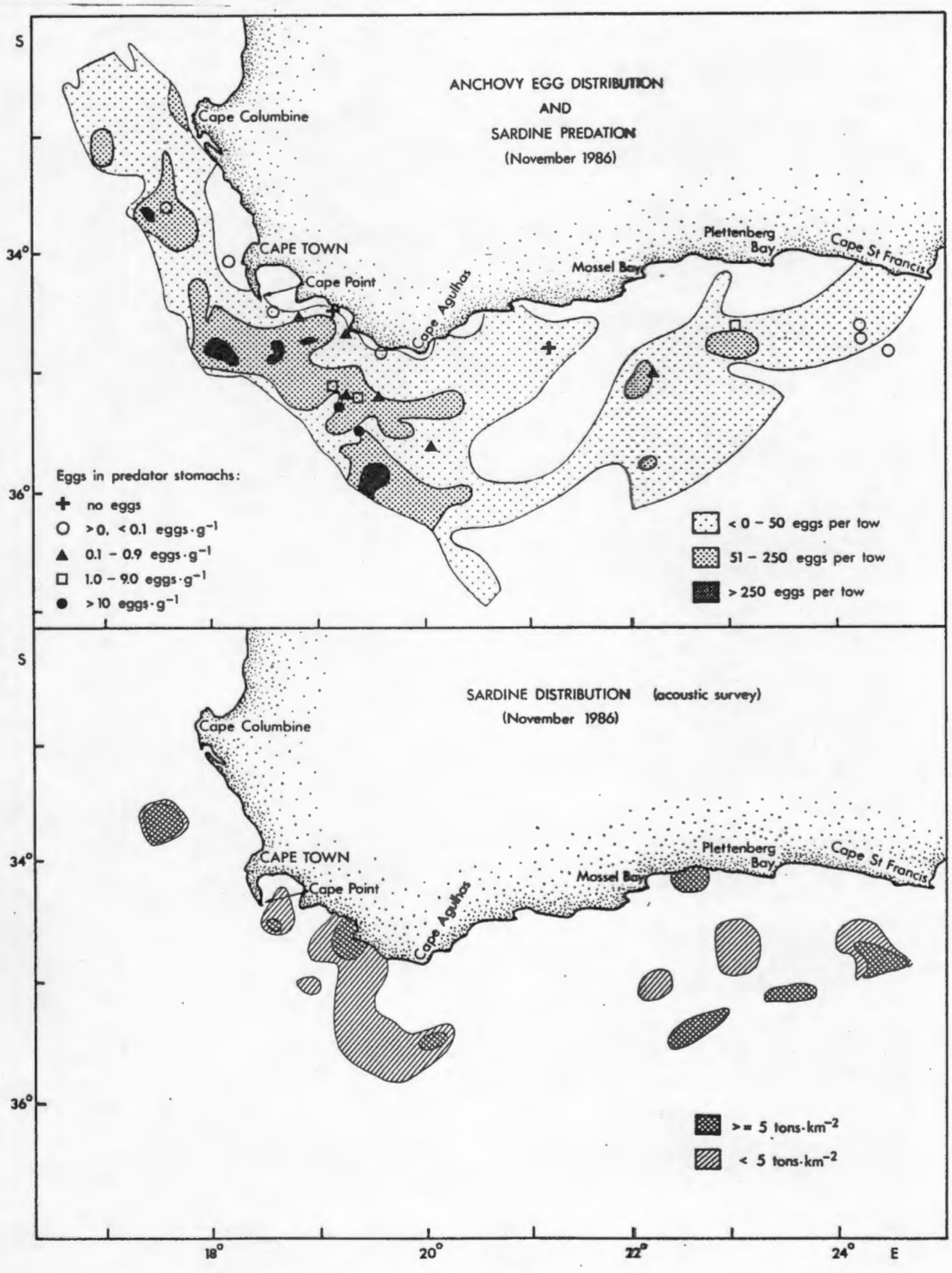


Fig. 2 Anchovy egg distribution monitored by CalVET net sampling, distribution of sardine monitored by acoustics and the places where predation occurred.



mordax), by Santander *et al.* (1983) and Alheit (1987) for the Peruvian anchovy *(Engraulis ringens)* and by Valdes *et al.* (1987) for the Cape anchovy. Thus,

$$C = EE \cdot g \cdot t \qquad (1)$$

where C is the mean number of eggs eaten per kilogramme of fish during time t, EE is the mean number of eggs observed per kilogramme of predator stomach, t is the duration of feeding (h) and g is the rate of gastric evacuation.

Although equation (1) is derived assuming a steady state between ingestion and gastric evacuation during time t, and there was indeed an apparent trend in egg consumption with time (Chapters 3 and 4), it does provide a simple method for calculating the number of eggs eaten and allows comparison with estimated values found according to the same methodology in other ecosystems. Furthermore, although the anchovy diel feeding cycle exhibits two peaks, one at dawn and one at dusk (Chapters 3 and 4), fewer fish caught during daylight were available for analysis than fish taken at night. Therefore, the average number of anchovy eggs determined per predator stomach over 24 hours of sampling was used as an index for comparison. Santander *et al.* (1983) and Alheit (1987) also considered indices over 24 hours of feeding and calculated the average consumption over this period despite the Peruvian anchovy having only a single feeding peak, at midnight (Jarre *et al.* 1989). The hourly instantaneous rate of

gastric evacuation was assumed to be 0.701 h^{-1} as estimated by Hunter and Kimbrell (1980) for northern anchovy feeding on anchovy eggs.

Therefore, from the data on egg abundance per 1 Kg of predators (mean egg consumption per kilogramme of anchovy and sardine = 32.7, 1058; 42.8, 739; 15.3, 3537 for 1986, 1987 and 1988 respectively) and the relationship given in equation (1), the average daily consumption of anchovy eggs by 1 kg of adult anchovy was calculated as 550, 720 and 258 eggs for 1986, 1987 and 1988 respectively (Table IV). Daily sardine predation on anchovy eggs was also estimated by means of equation (1) and assuming the same rate of gastric evacuation of anchovy eggs (i.e. 0.701 h^{-1}). The average number of eggs eaten daily per kilogramme of sardine was 17800, 12433 and 59516 eggs for 1986, 1987 and 1988 respectively (Table IV).

The proportion of egg mortality caused by intraspecific and interspecific predation by anchovy and sardine on anchovy eggs during the 60-h period prior to hatching was calculated according to the method given by Hunter and Kimbrell (1980), but including the modification introduced by MacCall (1981) and used by Santander *et al.* (1983) and Alheit (1987) for the Peruvian anchovy, and by Valdes *et al.* (1987) for the Cape anchovy:

Table IV: Parameters, their values and the results of calculations to estimate daily predator egg consumption and the percentage of total anchovy egg mortality due to egg cannibalism and sardine predation (values for: W, R, S, B, Z in 1986 are taken from Armstrong *et al.* 1988, while those for 1987 and 1988 are taken from unpublished SFRI records).

PARAMETERS	VALUES					
	1986		1987		1988	
	ANCHOVY	SARDINE	ANCHOVY	SARDINE	ANCHOVY	SARDINE
W= Average Fish Weight (kg)	0.011700		0.011066		0.012024	
F= Average number of eggs spawned per female	5627		6490		5878	
R= Sex ratio	0.5530		0.5609		0.5446	
S= Average fraction of females spawning per day	0.0950		0.0801		0.0845	
B= Biomass from acoustics (kg)	1.747×10^9	1.600×10^8	1.460×10^9	1.270×10^8	1.106×10^9	1.170×10^8
Z= Instantaneous mortality rate for anchovy eggs	0.0115		0.0115		0.0165	
C= Average anchovy eggs eaten daily per 1 kg of predator	550	17800	720	12433	258	59516
C_t= Total anchovy eggs eaten daily (C x B)	10×10^{11}	28×10^{11}	10.5×10^{11}	16×10^{11}	3×10^{11}	7×10^{12}
G= Total daily anchovy egg production per 1 kg anchovy (F x R x S)/W	25266		26349		22497	
G_t= Total daily anchovy egg production (G x B)	4.4×10^{13}		3.8×10^{13}		2.5×10^{13}	
Z_C= Proportion of the anchovy egg production consumed by cannibalism or sardine predation (C_t/ G_t)	0.02	0.06	0.03	0.04	0.01	0.28
P_C= Proportion of anchovy egg mortality caused by anchovy or sardine predation	0.04	0.12	0.06	0.08	0.02	0.44-0.56 *

(*) Range values depend on whether the value of Z for 1986-1987 or 1988 was used.

$$P_c = (C_t/G_t)/(1-e^{-(t.z)}) \quad (2)$$

where t= 60 h, C_t is the daily total anchovy egg consumption by anchovy or sardine, G_t is the total daily anchovy egg production and z is the hourly instantaneous rate of egg mortality.

The results of the calculations to estimate the daily egg consumption by predators and the percentage of the total egg mortality inflicted by cannibalism and sardine predation are given in Table IV. Whereas sardine predation caused only 12% of the total anchovy egg mortality in 1986, this percentage increased to 56% in 1988.

IV. DISCUSSION

The phenomenon of anchovy egg predation by an guild clupeoid species is not unique to the Benguela system. Santander *et al.* (1983) and Alheit (1987) reported that predation by Pacific sardine *Sardinops sagax* on anchovy eggs had a greater effect on egg mortality than did anchovy egg cannibalism itself.

Hunter and Kimbrell (1980) estimated that 32.4% of the egg mortality of the northern anchovy could be attributed to egg cannibalism, although applying MacCall's (1981) modification the value would be 28%. Alheit (1987) has calculated a similar percentage (i.e. 22%) for the Peruvian anchovy. For the Benguela system, Valdes *et al.* (1987) estimated that egg cannibalism by

anchovy could cause an average of 70% of the total anchovy egg mortality daily at specific sites of high density of eggs. Nevertheless, in this paper it was shown that, at stations where guild clupeoid species co-occur, sardine predation can be potentially more causative of egg mortality than anchovy egg cannibalism (Tables I, II and III).

Comparing data from the Peruvian system (from Alheit, 1987; Table V) with data from the Benguela system (Tables I, II and III), it is noticeable that the average number of anchovy eggs found per kilogramme of adult anchovy is up to two orders of magnitude lower in the Benguela than in the Peruvian system, whereas predation by sardines, as reflected by the number of eggs found in fish stomachs, is up to one order of magnitude higher in the Benguela.

Both feeding periodicity (Chapters 3 and 4) and anchovy diet at spawning (Chapter 4) suggest that anchovy eggs are a substantial source of food for *E. capensis*. The fast rate of digestion of anchovy eggs by the northern anchovy (they become digested and unrecognizable at a rate of 50% per hour, Hunter and Kimbrell, 1980) emphasizes that even relatively small numbers of eggs recorded in the stomachs of a fish may represent a substantial daily egg consumption. However, the factor regulating egg consumption by anchovy would likely be the functional response to egg density at specific sites (Valdes, 1986).

TABLE V

PERUVIAN SYSTEM

Station with co-occurring anchovy and sardine

Mean number of eggs in stomachs per 1 kg wet fish mass

(after Alheit, 1987)

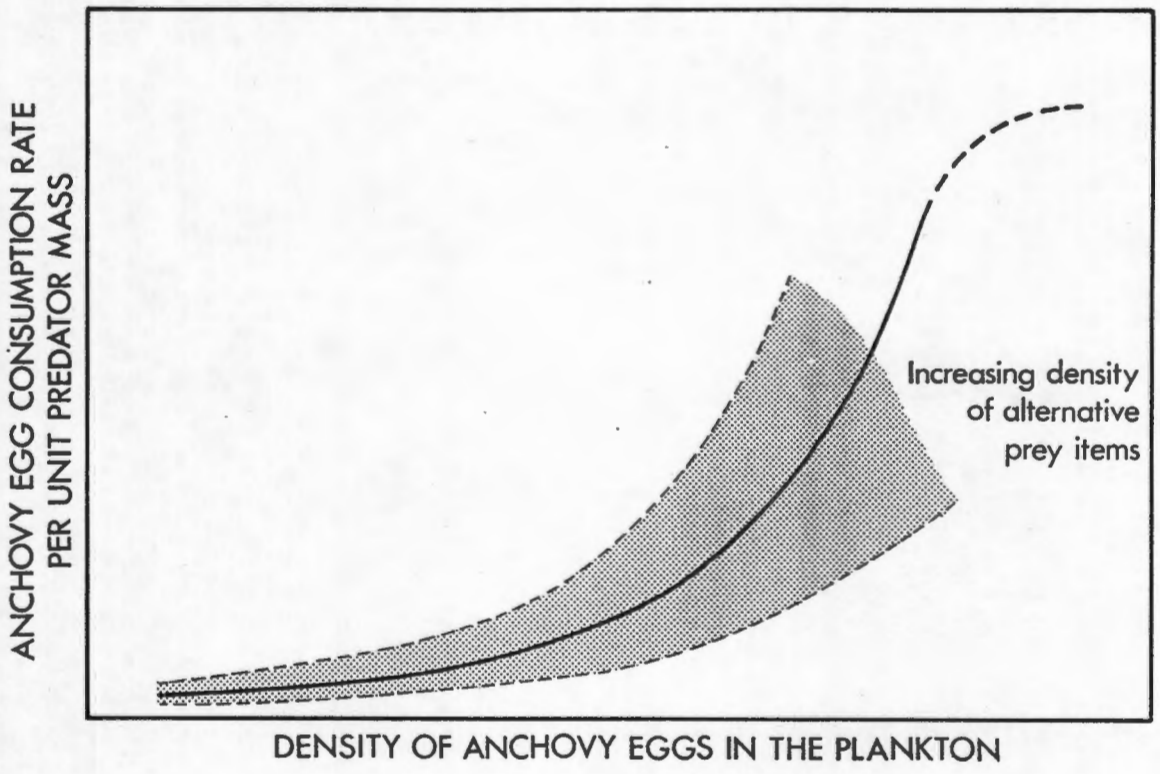
Collection	Anchovy	Sardine
6	69.1	99.0
10	46.5	40.1
12	124.6	1236.8
17	258.8	228.5
20	376.4	2593.5
23	209.8	215.3
31	358.6	1007.7
41	27.5	91.3
47	1718.3	1026.6
49	340.6	13.9
52	155.1	1781.2
Mean	355.0	757.0

The functional relationship between egg density and the egg consumption rate by individual anchovies, based on the work of Valdes (1986) and Valdes *et al.* (1987), is given in Figure 3. Given the similar feeding behaviour of the sardine to the anchovy, the same relationship may also apply to the sardine. The relationship that emerges from comparing the stomach of midwater trawl samples of clupeoids and nearby plankton samples suggests an exponential relationship, as a part of an s-shaped curve, between the number of anchovy eggs in intraguild predator stomachs and the local density of eggs in the water column.

The sigmoid-type of curve found (Fig. 3) is similar to the type-III curve of Holling (1959). The response levels off at high densities of prey because the predator becomes satiated and/or runs out of time in which to eat more prey (Murdoch and Oaten, 1975). Hence, the rate of food consumption eventually becomes limited by handling time and the rate of stomach evacuation (Peterman, 1977). Density-dependent mortality will result (Holling, 1959). The shape of the curve shown in Figure 3 varies according to the relative densities of eggs and other planktonic food organisms, such as copepods, which make up the bulk of the diet of anchovy and possibly also sardine when available (Chapters 3 and 4).

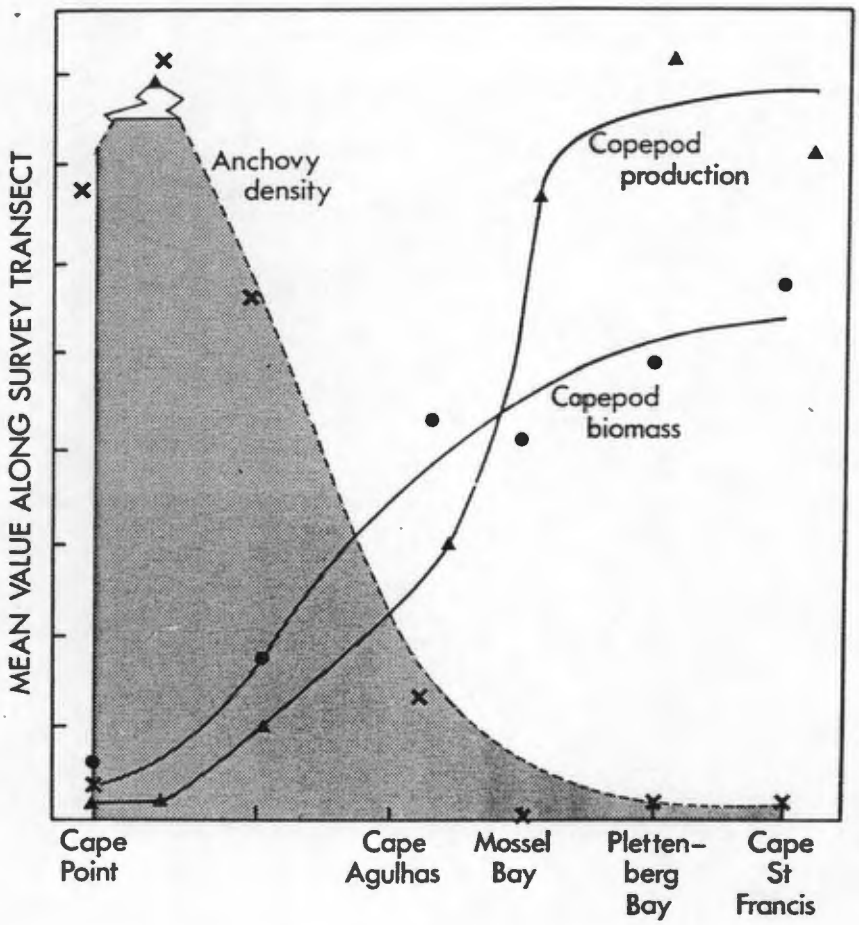
Davies (1957) suggested that the diet of sardine consisted of two-thirds phytoplankton and the remaining one-third zooplankton. However, he utilized a method of analysis based on the number of

Fig. 3 Functional relationship between anchovy egg density and anchovy egg consumption rate by individual fish (modified after Valdes, 1986).



food items rather than on volumetric analysis. Cushing (1978) reviewing the work of Davies (1957), postulated that the importance of zooplankton to the diet of sardine would have been greater if a volumetric method had been applied. Cushing further suggested that sardine is a size-selective feeder, preferring zooplankton. James (1988) also suggested that sardine is a zoophagous fish, but his statement was based on unpublished data. Some 90% of the zooplankton component of the sardine's diet reported by Davies (1957) was copepods (Chapter 3). However, from dietary analyses performed on sardines caught during the peak spawning period of anchovy, when secondary production seems to be low, it was found that phytoplankton was more abundant than zooplankton in the sardine's stomachs, and its presence could be related to the presence of anchovy eggs (Valdes, unpubl.). From Figure 4 it is clear that densities of spawning anchovy tend to be highest over the mid-shelf region of the western Agulhas Bank. Nevertheless the abundance and production of copepods there are low because of deep thermoclines and the resultant low primary production. Hence, rates of cannibalism and predation on clupeoid eggs are likely to be highest in this region. Furthermore, because sardine filter larger volumes of seawater than anchovy, if they exhibit a sort of Holling's (1959) functional response, their potential to prey on anchovy eggs in certain areas (i.e. over the western Agulhas Bank) is likely to cause greater mortality of anchovy eggs than cannibalism by anchovies.

Fig. 4 Anchovy density in the Benguela system and the availability of alternative prey items (modified after Peterson and Hutchings, 1989).



The data given in Tables I, II and III show that sardine predation is more destructive of anchovy eggs than anchovy cannibalism at stations where both species co-occur. However, the overall impact of sardine predation on anchovy eggs may depend on the one hand on the density of anchovy eggs, and on the other on the predator's numerical response (Murdoch, 1969; Murdoch *et al.* 1975).

In Chapter 2 a model was derived to estimate anchovy recruitment. The model's hypothesis is based on the existence at the egg stage of compensatory mechanisms which, at least potentially, may contribute largely to mortality. These mechanisms are: 1) cannibalism of adult anchovies on their own eggs; 2) predation by sardines on the same eggs. The existence of this interaction between guild species was considered (Chapter 2) likely to be the most important factor affecting survival to recruitment in anchovy. It would also, to a large degree, affect interannual variability in anchovy recruitment and, thus, the biomass of the anchovy population. Hence, it may cause variations in abundance of both clupeoid species.

The vulnerability of larvae of Cape anchovy and northern anchovy to cannibalism was investigated by Brownell (1985) and Folkvord and Hunter (1986) respectively and found to be an important source of mortality. Butler and Pickett (1988) discussed predation by adult northern anchovy on Pacific sardine larvae and its implication in recruitment variability. Adult Cape anchovy

have also been found to prey on sardine eggs (Valdes, unpubl.). The importance of such predation at times when the sardine biomass is higher than anchovy depends on whether compensatory mortality similar to anchovy cannibalism and sardine predation on anchovy eggs operates or not in the sardine. If intraguild predation by anchovy on sardine eggs and sardine cannibalism occur, such density-dependent mechanisms in both species may explain long-term clupeoid fluctuations in the Benguela and similar ecosystems.

The overall consumption of anchovy eggs by sardines in 1986 was three times greater than by anchovy, even though the sardine biomass was an order of magnitude lower than the anchovy biomass (Table IV). In 1987, the rate of anchovy cannibalism increased whereas that of sardine predation decreased. Then, in 1988, the proportion of the anchovy egg production consumed by sardines sharply increased whereas that by cannibalism dropped (Table IV). These results encompass the hypotheses of Chapter 2. Briefly, the frequencies of cannibalism and intraguild predation change according to the relative abundances of the predator and the prey species, their concentrations and the extent of their habitat overlap.

In 1986 the index of overlapping was relatively high and the concentration of both species was also relatively higher than in 1987 and 1988 (Chapter 2). On this basis it was expected, according to the results in Chapter 2, that predation by sardine would predominate over anchovy cannibalism in 1986 more than in

1987 and 1988. The values calculated supported this expectation: namely 12% of the total anchovy egg mortality was caused by sardine predation and 4% by cannibalism in 1986 (Table IV). According to the concentration of both species, it was expected to find higher values of sardine predation on anchovy eggs where both species co-occurred in 1986 (because in these areas, sardine predation operates mainly as a compensatory mortality, see Chapter 2) than in 1987 or 1988. The average number of anchovy eggs found per kilogramme of sardine mass (1988 eggs) was indeed relatively higher than in 1987 (Table I).

In 1987, both the index of species overlap and the concentration of each species decreased (Chapter 2). Therefore, sardine predation was expected to be relatively less influential in comparison with anchovy cannibalism as a source of egg mortality than it was in 1986 (Chapter 2). The percentage of anchovy egg mortality caused by sardine predation and by anchovy cannibalism were 8 and 6% respectively in 1987 (Table IV). According to the concentration of the species, predation by sardine should have been lower (Chapter 2) at places of co-occurrence in 1987 than in 1986. The average number of anchovy eggs found per kilogramme of sardine was 549 (Table II), almost four times lower than in 1986.

In 1988, the index of overlapping was the lowest of the three years, but there was a higher concentration of both species than in 1987 (still lower than in 1986). In 1988 there seems to have been an exponential increase in sardine abundance (Chapter 2).

Despite the lower overlap, the effect of the concentration of predators in specific areas, considering the probable density-dependent nature of sardine predation on anchovy eggs, means that higher values of sardine predation than in 1987 and 1986 were anticipated. The percentage of the total anchovy egg mortality caused by sardines was 56% (Table IV). Because a density-dependent sardine predation response is influenced by both increased density of prey (i.e. anchovy eggs) and density of predators (i.e. sardine), the actual number of anchovy eggs per kilogramme of sardine found in 1988 was higher than in either of the previous two years (3189 eggs, Table III). In terms of the percentage of anchovy egg production consumed by sardines, in 1988 it had risen to 28% compared to 6% and 4% in 1986 and 1987 respectively (Table IV).

In conclusion, the results have indicated that, to assist in managing such dynamic resources as the sardine and the anchovy, it may be appropriate to monitor the diet of both species to assess the survival of their respective embryonic stages when subjected to sardine predation or anchovy cannibalism. The anchovy stock-recruitment relationship may be strongly dome-shaped because of cannibalism in some areas (Valdes *et al.* 1987). However, cannibalism alone cannot be the sole mechanism affecting abundance of anchovy (Smith *et al.* 1989), and it may be scarcely noticeable as a cause of variation in the presence of the known environmental variability (MacCall, 1981). With the size of the sardine stock increasing, both intraspecific and interspecific predation likely have a

synergistic effect, causing fluctuations in anchovy recruitment and, hence, in anchovy stock size. Together, they may well be major causes of cycles in clupeoid abundances in the Benguela system.

ACKNOWLEDGEMENTS

The manuscript was greatly improved in style and content by careful reviews kindly provided by Dr. A.I.L. Payne (SFRI) and by my supervisor Professor Charles Griffiths (UCT). Tony Van Dalsen and his staff (SFRI) are thanked for the artwork. The work is being submitted in partial fulfilment of the requirements of a Ph D degree at the University of Cape Town.

REFERENCES

ALHEIT, J. 1987 - Egg cannibalism versus egg predation: their significance in anchovies. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 467-470.

ARMSTRONG, M.J., SHELTON, P.A., HAMPTON, I., JOLLY, G. and Y.C. MELO 1988 - Egg production estimates of anchovy biomass in the southern Benguela system. *Rep. Calif. coop. oceanic Fish. Invest.* 29: 137-157.

BROWNELL, C.L. 1985 - Laboratory analysis of cannibalism by larvae of the Cape anchovy *Engraulis capensis*. *Trans. Am. Fish. Soc.* 114(4): 512-518.

BUTLER, J.L. and D. PICKETT 1988 - Age-specific vulnerability of Pacific sardine, *Sardinops sagax*, larvae to predation by northern anchovy, *Engraulis mordax*. *Fishery Bull. Wash.* 86(1): 163-167.

CASWELL, H. 1978 - Predator-mediated coexistence: a nonequilibrium model. *Am. Naturalist* 112 (983): 127-154.

CUSHING, D.H. 1978 - Upper trophic levels in upwelling areas. In *Upwelling Ecosystems*. Boje, R. and M. Tomczak (Eds). New York; Springer: 101-110.

DAVIES, D.H. 1957 - The South African pilchard (*Sardinops ocellata*). Preliminary report on feeding off the West Coast, 1953-56. *Investl Rep. Div. Fish. S. Afr.* 30: 40 pp.

FOLKVORD, A. and J.R. HUNTER 1986 - Size-specific vulnerability of northern anchovy, *Engraulis mordax,* larvae to predation by fishes. *Fishery Bull. Wash.* 84: 859-869.

FOX, L.R. 1975 - Cannibalism in natural populations. *A. Rev. Ecol. Syst.* 6: 87-106.

HOLLING, C.S. 1959 - The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* 91: 293-320.

HUNTER, J.R. and C.A. KIMBRELL 1980 - Egg cannibalism in the northern anchovy, *Engraulis mordax. Fishery Bull., Wash.* 78(3): 811-816.

JAMES, A.G. 1988 - Are clupeid microphagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. *S. Afr. J. mar. Sci.* 7: 161-177.

JARRE, A., PALOMARES, M.L., SORIANO, M.L., SAMBILAY, V.C. and D. PAULY 1989 - Some improved analytical and comparative methods for estimating the food consumption of fishes. In *Proceedings of the ICES Symposium on Multispecies Models relevant to Management of Living Resources, Den Haag,*

Netherlands, October 1989 **Paper 12:** 19pp.

LASKER, R. and A.D. MacCALL 1983 - New ideas on the fluctuations of the clupeoid stocks off California. In *Proceedings of the Joint Oceanographic Assembly 1982: General Symposia.* Ottawa; Canadian National Committee/Scientific Committee on Oceanic Research: 110-120.

MacCALL, A.D. 1981 - The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis.* In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, 1980.* Sharp, G.D. (Conv. Ed.). Paris; Unesco: 201-220 (*I.O.C. Workshop Rep.* 28).

MacCALL, A.D. 1983 - Variability of pelagic fish stocks off California. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose, Costa Rica, April 1983.* Sharp, G.D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* **291**(2): 101-112.

MOSER, H.G. and E.H. AHLSTROM 1985 - Staging anchovy eggs. In *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, Engraulis mordax.* Lasker, R. (Ed.). *Tech. Rep. NOAA* **NMFS** 36: 37-41.

MURDOCH, W.W. 1969 - Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecol. Monogr.* 39: 335-354.

MURDOCH, W.W., AVERY, S. and SMYTH, M.E.B. 1975 - Switching in predatory fish. *Ecology* 10: 338-342.

MURDOCH, W.W. and A. OATEN 1975 - Predation and population stability. *Adv. ecol. Res.* 9: 1-385.

PETERMAN, R.M. 1977. A simple mechanism that causes collapsing stability regions in exploited salmonid populations. *J. Fish. Res. Bd Can.* 34: 1130-1142.

PETERMAN, R.M. and M. GATTO 1978 - Estimation of functional responses of predators on juvenile salmon. *J. Fish. Res. Bd Can.* 35: 797-808.

PETERSON, W.T. and L. HUTCHINGS 1989 - Clorophyll, particle spectra, zooplankton biomass and production in relation to hydrography and anchovy spawners on the Agulhas Bank. In *Proceedings of the Plankton Dynamics Mini-symposium, Cape Town, South Africa, May 1989. B.E.P. Rep.* 17: 81-95.

POLIS, G.A., MYERS, A. and R.D. HOLT 1989 - The ecology and evolution of intraguild predation: potential competitors that eat each other. *A. Rev. Ecol. Syst.* 20: 297-330.

RICKER, W.E. 1958 - Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Bd Can.* 119: 300 pp.

RICKER, W.E. 1973 - Linear regressions in fishery research. *J. Fish. Res. Bd Can.* 30(3): 409-434.

SANTANDER, H., ALHEIT, J., MacCALL, A.D. and A. ALAMO 1983 - Egg mortality of the Peruvian anchovy (*Engraulis ringens*) caused by cannibalism and predation by sardines (*Sardinops sagax*). In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San Jose, Costa Rica, April 1983.* Sharp, G.D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* 291(3): 1012-1025.

SHANNON, L.V., CRAWFORD, R.J.M., BRUNDRIT, G.B. and L.G. UNDERHILL 1988 - Responses of fish populations in the Benguela ecosystem to environmental change. *J. Cons. perm. int. Explor. Mer* 45(1): 5-12.

SMITH, P.E., FLERX, W. and R.P. HEWITT 1985 - The CalCOFI vertical egg tow (CalVET) net. In *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, Engraulis mordax.* Lasker, R. (Ed.). *Tech. Rep. NOAA* NMFS 36: 27-32.

SMITH, P.E., SANTANDER, H. and J. ALHEIT 1989 - Comparison of the

mortality rates of Pacific sardine *Sardinops sagax*, and Peruvian anchovy, *Engraulis ringens*, eggs off Peru. *Fishery Bull., Wash.* **87**: 497-508.

VALDES, E. 1986 - Egg cannibalism by anchovy in the Southern Benguela Current region. M.Sc. thesis. University of Cape Town: 85 pp.

VALDES, E.S., SHELTON, P.A., ARMSTRONG, M.J. and J.G. FIELD 1987 - Cannibalism in South African anchovy: egg mortality and egg consumption rates. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* **5**: 613-622.

WALTERS, C.J., STOCKER, M., TYLER, A.V. and S.J. WESTRHEIM 1986 - Interaction between Pacific cod (*Gadus macrocephalus*) and herring (*Clupea harengus pallasi*) in the Hecate Strait, British Columbia. *Can. J. Fish. aquat. Sci.* **43**(4): 830-837.

WELCH, D.W. 1986 - Identifying the stock-recruitment relationship for age-structured populations using time-invariant matched linear filters. *Can. J. Fish. aquat. Sci.* **43**: 108-123.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

In Chapter 1, the interannual variability of batch fecundity was studied. To conduct this study it was necessary to estimate reproductive parameters and, hence, the egg production per female Cape anchovy. As clupeoids, anchovy are characterized by extremely high fecundity, which is linearly proportional to the ovary-free weight of females. It was suggested in Chapter 1 that population mean egg production has been stable from 1986 to 1988 in the peak spawning season. However, by inference from experimental studies conducted on the relationship between fecundity and food supply by other researchers, it is likely that food supply is an important factor controlling fecundity (Scott, 1962). If so, there is potential for variation in fecundity to compensate for major changes in stock size, as proposed for plaice *Pleuronectes platessa* by Horwood *et al.* (1986).

The fact that no interannual variations were detected in the population mean fecundity of Cape anchovy at peak spawning, despite a potential decline in stock size suggests that either fecundity is a density-independent mechanism or that egg size could compensate for stock changes and be a reflection of food supply. Normally there is an annual seasonal decline in egg size in northern anchovy and other clupeoids (Blaxter, 1969; De Ciechomski, 1973; Le Clus, 1979; Hunter and Leong, 1981). Production of smaller eggs may be an energy-conserving mechanism whereby fecundity is maintained constant, but at a lower reproductive effort. Hislop *et al.* (1978) found that eggs

produced by haddock *Melanogrammus aeglifinus* in the laboratory tended to be smaller in females fed a lower ration.

Also in Chapter 1, it was suggested that changes in egg size could be compensating for a variation in the size of the anchovy stock. However, the suggestion was of dubious value because it originated from an upward response found in the gonadosomatic index (GSI) while batch fecundity and relative fecundity were unchanged. Because the GSI depends on, among other things, how long before spawning the females were caught, the upward response in GSI could have been attributable to differences in the stages of hydration of the eggs in the fish sampled, rather than to changes in egg size. Finally, Chapter 1 concluded that batch fecundity was probably not compensating for changes in stock size and that although egg size could compensate, it was considered to be an unlikely cause. It was then suggested that higher rates of cannibalism might be compensating for a lower food supply (Chapters 1, 4 and 5).

If there is variation in egg size in Cape anchovy as a result of a variable food supply, there could also be variable rates of cannibalism. Cannibalism is mainly associated with filtration (Hunter and Kimbrell, 1980; MacCall, 1981; Chapter 4) and, because anchovy eggs lie at the upper size limit associated with filtration activity (James, 1987), it seems that, if egg size were to decrease during periods of food scarcity, more eggs might be consumed by filtration. Hence, reduced egg size may be associated with increased rates of cannibalism by adults. Also,

as egg size would alter the survival potential of the larva (Blaxter and Hempel, 1963), a cannibalistic mechanism removing the smaller eggs could have important consequences to selection (Chapter 4).

In Chapter 2, a model was postulated suggesting that egg cannibalism by anchovy and predation on anchovy eggs by sardine possibly determine the level of anchovy recruitment. In the model, numbers of eggs of both species were used as an index of the abundance of guild clupeoid species. A model of the Ricker (1954, 1958) type was run to estimate anchovy recruitment from 1984 to 1988 under variable conditions of egg density and habitat overlap between both species. Those estimates were highly correlated with observed values of recruitment determined acoustically.

The idea of the model was based on Fox (1975), who suggested that a balance between cannibalism and predation influences the coexistence patterns of competing species. In the case of anchovies and sardines, both compete for the same resources in the Benguela ecosystem (James, 1988) and they have fluctuated naturally over many years (Shackleton, 1987; Shannon *et al.* 1988). Observations made during 1984 and 1985 (Valdes *et al.* 1987) supported the observations reported by Bailey and Houde (1989) on *Engraulis spp.* in other ecosystems, namely that all species exhibit high rates of cannibalism on their own eggs. This same set of data (Valdes *et al.* 1987; Valdes, unpubl.) revealed predation by sardines on anchovy eggs. Chapter 5 reported on the rates of cannibalism and sardine predation on the basis of data

collected during 1986, 1987 and 1988. Interspecific predation by sardine on anchovy eggs can be a form of competition (Polis *et al.* 1989) additional to that between the two species for resources and/or space. If food is in short supply for the entire assemblage of anchovies and sardines (Shannon and Field, 1985; Peterson and Hutchings, 1989), it is not surprising to find predation among both conspecific and heterospecific competitors (Fox, 1975).

Whatever the relative abundance of the guild species, rates of cannibalism should be highest for guild species without intraguild predators or close competitors (Fox, 1975), i.e. situations in which the habitat overlap is low between anchovy and sardine. In Chapter 2 it was assumed that as a larger proportion of a species' habitat would be shared, interspecific events would increase, and most compensatory mortality would be caused by sardine predation. However, common species may always cannibalize to some extent even when interspecific competition (i.e. predation) is high (Chapter 5), although the proportion of cannibalistic events in this case would be lower than if there were less overlap (Fox, 1975).

It was suggested in Chapter 4 that cannibalism is not an aberrant behaviour limited to confined or highly stressed populations, but a normal response to many environmental factors. The relative availability of alternative food, the density of both adults and eggs, and food deprivation or crowding may all influence the intensity of this behaviour (Fox, 1975; Chapters 4 and 5).

The spawner-recruit model of Ricker (1954, 1958) is based on the concept of compensatory mortality (increasing mortality with increasing density) of pre-recruits. In such a domed spawner-recruit model, the causes of density-dependent mortality are believed to result from aggregation of predators or cannibalism (Cushing, 1975; MacCall, 1981). Valdes (1986) and Valdes *et al.* (1987) found empirical evidence of compensatory mortality for the Cape anchovy.

Based on the evidence for compensatory mortality, a Ricker-type model based on Csirke (1980) was postulated for Cape anchovy in Chapter 2. Egg abundances were taken as stock-size indices and density-dependent parameters were related to density and to habitat overlap of both guild clupeoid species. The model suggested that those factors potentially lead to fluctuations in anchovy recruitment, and hence, to the biomass of the stock. The hypotheses postulated in the model regarding the importance of compensatory density-dependent mortality (by cannibalism and sardine predation) of the early life stages of fish, were supported in Chapter 5.

MacCall (1981) for the northern anchovy and Valdes (1986) for the Cape anchovy expressed the opinion that cannibalism by anchovy on eggs is an important regulatory mechanism that depends on adult stock density and could produce a Ricker-type (dome-shaped) spawner-recruit curve. However, MacCall (1981) concluded that density-independent factors tend to mask these relatively weak density-dependent influences. Welch (1986) used statistical

filtering to remove density-independent factors affecting recruitment in 16 stocks of eight species and improved the resulting stock-recruitment relationships in every case.

In Chapter 5 it was indicated that the anchovy stock-recruitment relationship may be strongly dome-shaped due to cannibalism at specific sites (Valdes *et al.* 1987). Nevertheless, in the total area of anchovy distribution, cannibalism alone seemed not to be the only mechanism effecting anchovy recruitment. It was then suggested (Chapter 5) that the presence of an increasing stock size of sardine would likely cause a synergistic effect, interspecific and intraspecific predation resulting in a reduced anchovy recruitment. Hence, both mechanisms together would likely cause recruitment variability, supporting the postulation in Chapter 2.

Smith's (1985) simulation studies of northern anchovy also supported the model of Chapter 2. He examined the sensitivity of recruitment to changes in the parameters of mortality, growth and duration of pre-recruit life-stages. He concluded that moderate changes in mortality of eggs and larvae could easily account for five-fold increases or decreases in recruitment. He further concluded that, although a moderate increase in juvenile mortality could also account for a five-fold decrease in anchovy recruitment, no reasonable change in juvenile mortality rate could cause a five-fold increase.

If the scenario suggested by previous chapters is borne in mind,

i.e. that egg production varies much less than the spawning stock biomass (Chapter 1) and that most density-dependent mortality occurs at the egg stage (Chapters 2, 4 and 5), it can be concluded that the causes of variability in recruitment mostly take place at that life stage in the Cape anchovy. Therefore, the regulation in this pre-recruitment phase (by intraspecific and/or interspecific predation on eggs) may be critical to anchovy recruitment. Consequently, the hypothesis that mortality by predation is a key factor to recruitment, as postulated by Ware (1975), Shepherd and Cushing (1980) and Sissenwine (1984), has been strengthened with the results of the present study. On the other hand, other hypotheses, such as that starvation mortality determines recruitment (Nellen, 1986) have yet to be confirmed (Oiestad, 1983; Sissenwine, 1984).

In Chapter 3, the results of a study on the abundance, diet and food consumption rate of Cape anchovy and implications to whether or not there is food limitation for pelagic fish in the Benguela ecosystem were discussed. The daily rate of anchovy consumption was used in Chapter 4 to estimate the energetics of intraspecific predation. It was concluded that intraspecific predation actually means an overall gain of energy for the anchovy stock (permitting reproduction) and the implications of this for selection were discussed.

In Chapter 4, the results presented indicate that, given the scarcity of secondary production available to Cape anchovy at the time of spawning, anchovy may very well have to feed on their

eggs in order to reproduce successfully. Therefore, it seemed likely that cannibalism on eggs has become an essential feature of anchovy life history. High fecundity allows for such a behaviour (Nellen, 1986). Because such cannibalistic behaviour was also exhibited at the larval stage in Cape anchovy (Brownell, 1985; White, 1988; O'Toole *et al.* in prep.), recruitment failures may be strongly correlated with the intensity of the mortality inflicted by cannibalism and predation. Therefore, the hypothesis that high mortality could be due to larval starvation (Cushing, 1970, 1975; Lasker, 1975) would again receive less support.

In conclusion, this thesis postulates that, when the anchovy and the sardine populations interact with each other, their responses to exploitation cannot be predicted from classical studies of single-species dynamics. In this sense, the development of the predator-prey interaction model of Chapter 2 could be of importance in studying the effect of exploitation on both species.

Although the significance of a three-parameter-model fitted to five data points (Chapter 2) might be doubtful, the model has shown the importance of making use of available time-series in identifying those factors potentially affecting anchovy egg survival, and hence anchovy recruitment. Such effects cannot be predicted by simple addition, because they interact in a rather complex manner. Rather, it is necessary for them to be integrated in a model.

The model in Chapter 2 needs to be validated in future by testing

its prediction of annual anchovy recruitment according to (i) the variation in egg densities of anchovy and sardine; (ii) the extent of habitat overlap between them and (iii) the relative abundance of both species. Data for 1984-1988 support the model, showing a high correlation between recruitment of anchovy derived from acoustic surveys and recruitment predicted by the model.

Because the model performs well with the data for the years 1984-1988, the suggestion is that interannual changes in recruitment are not mere coincidence of factors in the short time-series or the results of environmental forcing affecting the species in opposite directions, as proposed by Walters *et al.* (1986). On the contrary, the model has shown that such factors (egg density, the extent of habitat overlap, species abundance) combined in the manner proposed in Chapter 2 may cause variations in compensatory mortality, which probably determines the level of anchovy recruitment. Such compensatory mortality is concluded to be mainly the result of anchovy cannibalism and sardine predation (Chapters 2 and 5).

Conventional theories of fisheries management have considered only the steady state of a system. The importance of the stability of the system to fisheries management was initially discussed in the mid 1970s by researchers such as Jones and Walters (1976), Peterman (1977) and Clark and Mangel (1979). Shirakihara and Tanaka (1981) suggested that a maximum sustainable yield (MSY) policy might be inappropriate in the light of the known instability of systems. In Chapter 2, it was shown that

the anchovies and sardines do not collectively constitute a stable system and that cannibalism and predation may lead to oscillations in year-class strength. Thus, they may be responsible for the large fluctuations suffered by clupeoid species in the Benguela and other similar ecosystems (Kawasaki and Omori, 1988; Shannon *et. al.* 1988, Crawford *et. al.* in press).

Obviously there is a conflict between a policy exploiting the maximum catch of the prey and one exploiting the maximum catch of the predator (Larkin, 1977; Shirakihara and Tanaka, 1981). Empirical evidence for sardine being the predator and anchovy the prey in the Benguela system was given in Chapter 5. It seems clear that independent application of MSY (or similar) policies for each of the two interacting populations would be impossible. It is therefore appropriate to suggest that a future investigation be made into the feasibility of applying a multi--species management plan for anchovy and sardine in the Benguela ecosystem. Such a plan could achieve better management of the fishery for both species.

ACKNOWLEDGEMENTS

This chapter concludes the thesis. I wish to acknowledge -without naming them- all the people that have contributed to the various stages of development of this thesis. I sincerely thank Dr. R. Melville-Smith and Dr. A.I.L. Payne (SFRI) and Professor C. Griffiths (UCT) for improving the contents and the English by careful reviews of the various drafts. Specially I thank again

my supervisor Professor Charles Griffiths (UCT) for his guidance, patience, continuous encouragement throughout all the thesis. Also I am grateful to the Director of Sea Fisheries Research Institute (SFRI) for his permission to use the results for a Ph D thesis.

REFERENCES

BAILEY, K.M. and E.D. HOUDE 1989 - Predation on eggs and larvae of marine fishes and the recruitment problem. *Adv. mar. Biol.* 25: 1-83.

BLAXTER, J.H.S. 1969 - Development: eggs and larvae. In *Fish Physiology* 3. Hoar, W.S. and D.J. Randall (Eds). New York; Academic Press: 178-252.

BLAXTER, J.H.S. and G. HEMPEL 1963 - The influence of egg size on herring larvae (*Clupea harengus* L.). *J. Cons. perm. int. Explor. Mer* 28: 211-240.

BROWNELL, C.L. 1985 - Laboratory analysis of cannibalism by larvae of the Cape anchovy *Engraulis capensis*. *Trans. Am. Fish. Soc.* 114(4): 512-518.

CLARK, C.W. and M. MANGEL 1979 - Aggregation and fishery dynamics: a theoretical study of schooling and the purse seine tuna fisheries. *Fishery Bull., Wash.* 77: 317-337.

CRAWFORD, R.J.M., SIEGFRIED, W.R., SHANNON, L.V., VILLACASTIN-HERRERO, C.A. and L.G. UNDERHILL 1990 (in press) - Environmental influences on marine biota off southern Africa. *S. Afr. J. Sci.*

CSIRKE, J. 1980 - Recruitment in the Peruvian anchovy and its

dependence on the adult population. *Rapp. P-v. Reun. Cons. perm. int. Explor. Mer* 177: 307-313.

CUSHING, D.H. 1970 - The regularity of the spawning season of some fishes. *J. Cons. perm. int. Explor. Mer* 33: 81-97.

CUSHING, D.H. 1975 - The natural mortality of plaice. *J. Cons. perm. int. Explor. Mer* 36: 150-157.

DE CIECHOMSKI, J.D. 1973 - The size of the eggs of the Argentine anchovy, *Engraulis anchoita* (Hubbs & Marini) in relation to the season of the year and the area of spawning. *J. Fish Biol.* 5(3): 393-398.

FOX, L.R. 1975 - Cannibalism in natural populations. *A. Rev. Ecol. Syst.* 6: 87-106.

HISLOP, J.R.G., ROBB, A.P. and J.A. GAULD 1978 - Observations on effects of feeding level on growth and reproduction in haddock, *Melanogrammus aeglifinus* (L.) in captivity. *J. Fish Biol.* 13(1): 85-98.

HORWOOD, J.W., BANNISTER, R.C.A. and HOWLETT, G.J. 1986. Comparative fecundity of north sea plaice (*Pleuronectes platessa* L.). *Proc. R. Soc. Lond., Ser. B* 228: 401-431.

HUNTER, J.R. and C.A. KIMBRELL 1980 - Egg cannibalism in the northern anchovy, *Engraulis mordax. Fishery Bull., Wash.*

78(3): 811-816.

HUNTER, J.R. and R.J.H. LEONG 1981 - The spawning energetics of female northern anchovy, *Engraulis mordax*. *Fishery Bull., Wash.* 79(2): 215-230.

JAMES, A.G. 1987 - Feeding ecology, diet and field-based studies on feeding selectivity of the Cape anchovy *Engraulis capensis* Gilchrist. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 673-692.

JAMES, A.G. 1988 - Are clupeid microphagists herbivorous or omnivorous? A review of the diets of some commercially important clupeids. *S. Afr. J. mar. Sci.* 7: 161-177.

JONES, D.D. and C.J. WALTERS 1976 - Catastrophe theory and fisheries regulation. *J. Fish. Res. Bd Can.* 33: 2829-2833.

KAWASAKI, T. and M. OMORI 1988 - Fluctuations in the three major sardine stocks in the Pacific and the global trend in temperature. In *Long Term Changes in Marine Fish Populations*. Wyatt, T. and M.G. Larraneta (Eds). Vigo; Instituto de Investigaciones Marinas de Vigo: 37-53 (Proceedings of a symposium held in Vigo, November 1986).

LARKIN, P.A. 1977 - An epitaph for the concept of maximum sustained yield. *Trans. Am. Fish. Soc.* 106: 1-11.

LASKER, R. 1975 - Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fishery Bull., Wash.* 73(3): 453-462.

LE CLUS, F. 1979 - Dry mass of yolked oocytes of the South West African pilchard *Sardinops ocellata* in relation to maturity stages and spawning cycles, 1972 - 1974. *Investl Rep. Sea Fish. Brch S. Afr.* 119: 29 pp.

MacCALL, A.D. 1981 - The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis*. In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, 1980*. Sharp, G.D. (Conv. Ed.). Paris; Unesco: 201-220 (*I.O.C. Workshop Rep.* 28).

NELLEN, W. 1986 - A hypothesis on the fecundity of bony fish. *Meeresforschung* 31: 75-89.

OIESTAD, V. 1983 - Growth and survival of herring larvae and fry (*Clupea harengus* L.) exposed to different feeding regimes in experimental ecosystems: outdoor basin and plastic bags. Ph.D. thesis, University of Bergen: 299 pp.

O'TOOLE, M.J., ARMSTRONG, M.J. and I.HAMPTON (in preparation) - Observations on cannibalism by the South African anchovy (*Engraulis capensis*) on post-larvae and early juveniles.

PETERMAN, R.M. 1977 - A simple mechanism that causes collapsing stability regions in exploited salmonid populations. *J. Fish. Res. Bd Can.* 34: 1130-1142.

PETERSON, W.T. and L. HUTCHINGS 1989 - Chlorophyll, particle spectra, zooplankton biomass and production in relation to hydrography and anchovy spawners on the Agulhas Bank. Extended abstract. In *Proceedings of the Plankton Dynamics Mini-Symposium, Cape Town, May 1989. Rep. Benguela Ecol Progm. S. Afr.* 17: 81-95.

POLIS, G.A., MYERS, A. and R.D. HOLT 1989 - The ecology and evolution of intraguild predation: potential competitors that eat each other. *A. Rev. Ecol. Syst.* 20: 297-330.

RICKER, W.E. 1954 - Stock and recruitment. *J. Fish. Res. Bd Can.* 11: 559-623.

SCOTT, D.P. 1962 - Effect of food quantity on fecundity of rainbow trout *Salmo gairdneri*. *J. Fish. Res. Bd Can.* 19: 715-731.

SHACKLETON, L.Y. 1987 - A comparative study of fossil fish scales from three upwelling regions. In *The Benguela and Comparable*

Ecosystems. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 79-84.

SHANNON, L.V., CRAWFORD, R.J.M., BRUNDRIT, G.B. and L.G. UNDERHILL 1988 - Responses of fish populations in the Benguela ecosystem to environmental change. *J. Cons. perm. int. Explor. Mer* **45**(1): 5-12.

SHANNON, L.V. and J.G. FIELD 1985 - Are fish stocks food-limited in the southern Benguela pelagic ecosystem? *Mar. Ecol. Prog. Ser.* **22**(1): 7-19.

SHEPHERD, J.G. and D.H. CUSHING 1980 - A mechanism for density-dependent survival of larval fish as the basis of a stock-recruitment relationship. *J. Cons. perm. int. Explor. Mer* **39**: 160-167.

SHIRAKIHARA, K. and S. TANAKA 1981 - A predator-prey model for two-species populations with nonlinear interactions and implications for fisheries management. *Bull. japan. Soc. scient. Fish.* **47**(4): 487-493.

SISSENWINE, M.P. 1984 - Why do fish populations vary? In *Exploitation of Marine Communities*. May, R.M. (Ed.). Berlin, Springer: 59-94 (Report of the Dahlem Workshop on Exploitation of Marine Communities, Berlin, April 1984).

SMITH, P.E. 1985 - Year-class strength and survival of 0-group clupeoids. *Can. J. Fish. aquat. Sci.* **42**(Suppl. 1): 69-82.

VALDES, E. 1986 - Egg cannibalism by anchovy in the Southern Benguela Current region. M.Sc. thesis, University of Cape Town: 85 pp.

VALDES, E.S., SHELTON, P.A., ARMSTRONG, M.J. and J.G. FIELD 1987 - Cannibalism in South African anchovy: egg mortality and egg consumption rates. In *The Benguela and Comparable Ecosystems*. Payne, A.I.L., Gulland, J.A. and K.H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 613-622.

WALTERS, C.J., STOCKER, M., TYLER, A.V. and S.J. WESTRHEIM 1986 - Interaction between Pacific cod (*Gadus macrocephalus*) and herring (*Clupea harengus pallasi*) in the Hecate Strait, British Columbia. *Can. J. Fish. aquat. Sci.* **43**(4): 830-837.

WARE, D.M. 1975 - Relation between egg size, growth, and natural mortality of larval fish. *J. Fish. Res. Bd Can.* **32**: 2503-2515.

WELCH, D.W. 1986. Identifying the stock-recruitment relationship for age-structured populations using time-invariant matched linear filters. *Can. J. Fish. aquat. Sci.* **43**: 108-123.

WHITE, P.N. 1988 - Clupeoid piscivory and year class strength. In *Benguela Clupeoid Piscivory (Research Project 1987/1988)*.

Unpublished internal report, Dept of Zoology, University of Cape Town: 4 pp.

APPENDIX 1

The Benguela and Comparable Ecosystems
Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci. 5: 613-622*
1987

CANNIBALISM IN SOUTH AFRICAN ANCHOVY: EGG MORTALITY AND EGG CONSUMPTION RATES

E. S. VALDÉS†, P. A. SHELTON*, M. J. ARMSTRONG* AND J. G. FIELD†*

Cannibalism by adult anchovy on their eggs was investigated within an area of intensive spawning over the Agulhas Bank by comparing estimates of daily *per capita* egg production and consumption of eggs derived from repeated sampling of plankton by CalVET net dips and of fish by midwater trawl. Consumption of eggs over a 15-hour feeding period was estimated to have caused, on average, 70 per cent of the total egg mortality within the study area, although cannibalism was shown to be density-dependent.

Kannibalisme deur geslagsryp ansjovis van hul eiers is ondersoek in 'n gebied van intensiewe kuitskiet oor die Agulhasbank deur ramings van daaglikse *per capita*-eierproduksie en -inname van eiers afgelei uit herhaalde bemonstering van plankton met CalVET-nethale en van vis met 'n midwatertreil te vergelyk. Die inname van eiers oor 'n voedingstydperk van 15 h het na raming gemiddeld 70 persent van die totale eiermortaliteit binne die studiegebied veroorsaak, hoewel aangetoon is dat kannibalisme van digtheid afhanklik is.

Anchovy *Engraulis capensis* is currently the main contributor to the South African pelagic fishery. The fishery exploits mainly anchovy less than one year of age and is dependent upon a consistent run of recruits off the West Coast during autumn and winter. The population sizes of clupeoids are, however, notoriously variable (Murphy 1977, Blaxter and Hunter 1982, Lasker and MacCall 1983), fluctuations in year-class strength being determined largely by the survival rate during the pre-recruit stage (Smith 1985). Pre-recruit mortality operates on eggs, larvae and juveniles, the former two being planktonic and the latter nektonic. Mortality occurs from predation, starvation and disease (Lasker 1985), but starvation and predation are believed to be the dominant sources of natural mortality in pelagic fish (Smith and Lasker 1978). In addition, physical transport of pre-recruits out of the spawning/nursery area is also considered to be a major source of mortality, because surrounding waters are typically unfavourable for survival, although actual mortality may be due to predation or starvation (Smith and Lasker op. cit.). The offshore Ekman transport in the Benguela region during the peak of the upwelling season (coincident with the spawning time for anchovy) may carry eggs and larvae out of the system, and strong winds might dilute food patches through turbulent mixing within the water column, as found off California (Lasker 1975), causing increased mortality in pre-recruits.

Among the causes of egg mortality, egg cannibalism has been reported for clupeoid populations in various parts of the world, e.g. Argentinian anchovy *Engraulis anchoita* (De Ciechomski 1967), Japanese anchovy *E. japonicus* (Hayasi 1967), Californian anchovy *E. mordax* (Loukashkin 1970), Peruvian anchovy *E. ringens* (Rojas de Mendiola *et al.* 1969, Rojas de Mendiola and Ochoa 1973, Rojas de Mendiola 1981). Recently the importance of cannibalism as a source of mortality of eggs of *E. mordax* and *E. ringens* has been demonstrated by quantitative comparison of daily egg production with estimated rates of egg consumption (Hunter and Kimbrell 1980, MacCall 1981, Santander *et al.* 1983, Alheit 1987). Cannibalism on eggs of *E. mordax* was estimated to account for 20–28 per cent of the total egg mortality (MacCall op. cit.), and, in Peru, cannibalism by *E. ringens* caused 22 per cent of the total egg mortality (Alheit op. cit.).

The aim of this paper is to present the results of an investigation into the rate of egg cannibalism by anchovy within an area of intensive spawning activity off the south coast of South Africa.

METHODS

Anchovy stomach samples and plankton samples were collected on research cruises of the Sea Fisheries Research Institute's (SFRI) R.S. *Africana* in November 1984 and November/December 1985 over the Agulhas Bank. The cruises were arranged to coincide with the peak of the anchovy spawning season (Shelton 1986), because the main aim was to

* Sea Fisheries Research Institute, Private Bag X2, Rogge Bay, 8012, Cape Town
† Marine Biology Research Institute, Department of Zoology, University of Cape Town, Private Bag, Rondebosch, 7700, Cape Town
Manuscript received: November 1986

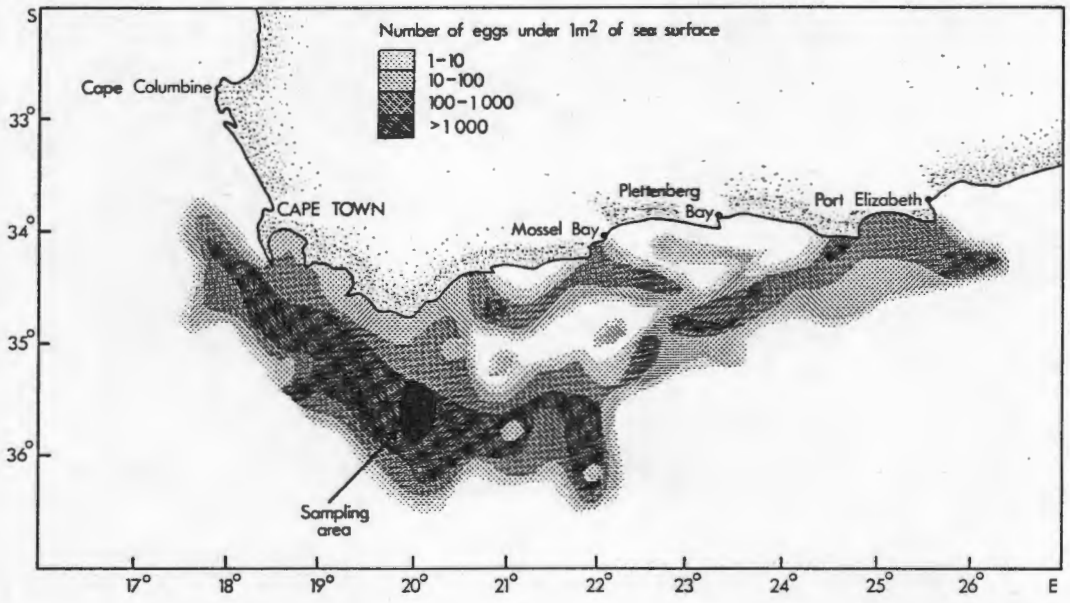


Fig. 1: Map of the anchovy egg distribution during November 1984 showing all the grid stations (after Shelton 1986) and the position of sampling for this study during 1984 and 1985

determine anchovy spawner stock biomass (Hampton *et al.* 1985).

Anchovy eggs were collected in 31 vertical hauls made with a CalVET (CalCOFI Vertical Egg Tow) net (Smith *et al.* 1985) from a depth of 200 m (or 10 m from the bottom if shallower) to the surface. Sampling took place over a period of four days at stations positioned within an area characterized by high densities of both eggs and spawning fish during the November 1984 cruise (Fig. 1), and a further nine hauls were made during the November 1985 cruise in roughly the same area. A "Universal Underwater Unit", designed by SFRI and containing a temperature probe and depth sensor connected to a microprocessor on board the vessel, was attached below the CalVET net. Thus, a record and a plot of the temperature/depth profile were available for each tow.

Immediately after the completion of each tow, the plankton sample was preserved in 4-per-cent buffered formaldehyde in seawater. In the laboratory, anchovy eggs were removed from the plankton samples under a binocular dissecting microscope at 20 × magnification. Based on the degree of embryonic development and following the method of Moser and Alhstrom (1985), eggs were assigned to 11 stages (Fig. 2). The abundance of each stage in the samples was standardized to the number under 1 m² of sea surface. The time of peak spawning was determined from the time of day at which newly fertilized eggs appeared in the egg collection and from observations of the occurrence of hydrated eggs in the ovaries of adult fish.

Data from incubation experiments carried out on board the ship in a thermal gradient incubator (King 1977) were used, together with *in situ* measurements of surface temperature (5 m), to estimate the approximate age of each stage in hours (Fig. 3). The surface temperature represented the maximum incubation temperature that eggs would be likely to encounter in the upper mixed layer. Generally, eggs from two or three previous nights' spawnings were present in each positive sample. The eggs in each developmental stage were assigned to one of these nights according to their estimated age. All the eggs in a sample which were assigned to a given night's spawning were then re-aged according to the difference between the time of sampling and the time of peak spawning (spawning occurs over a period of several hours each night, reaching a peak at approximately 21h00 [SFRI, unpublished data]). The data from the 31 stations were used to estimate hourly mortality rates by means of non-linear least-squares regression of abundance on age, using only eggs fully recruited to the plankton but not yet at the age of hatching.

Adult anchovy were collected by midwater trawl immediately preceding or following each CalVET net

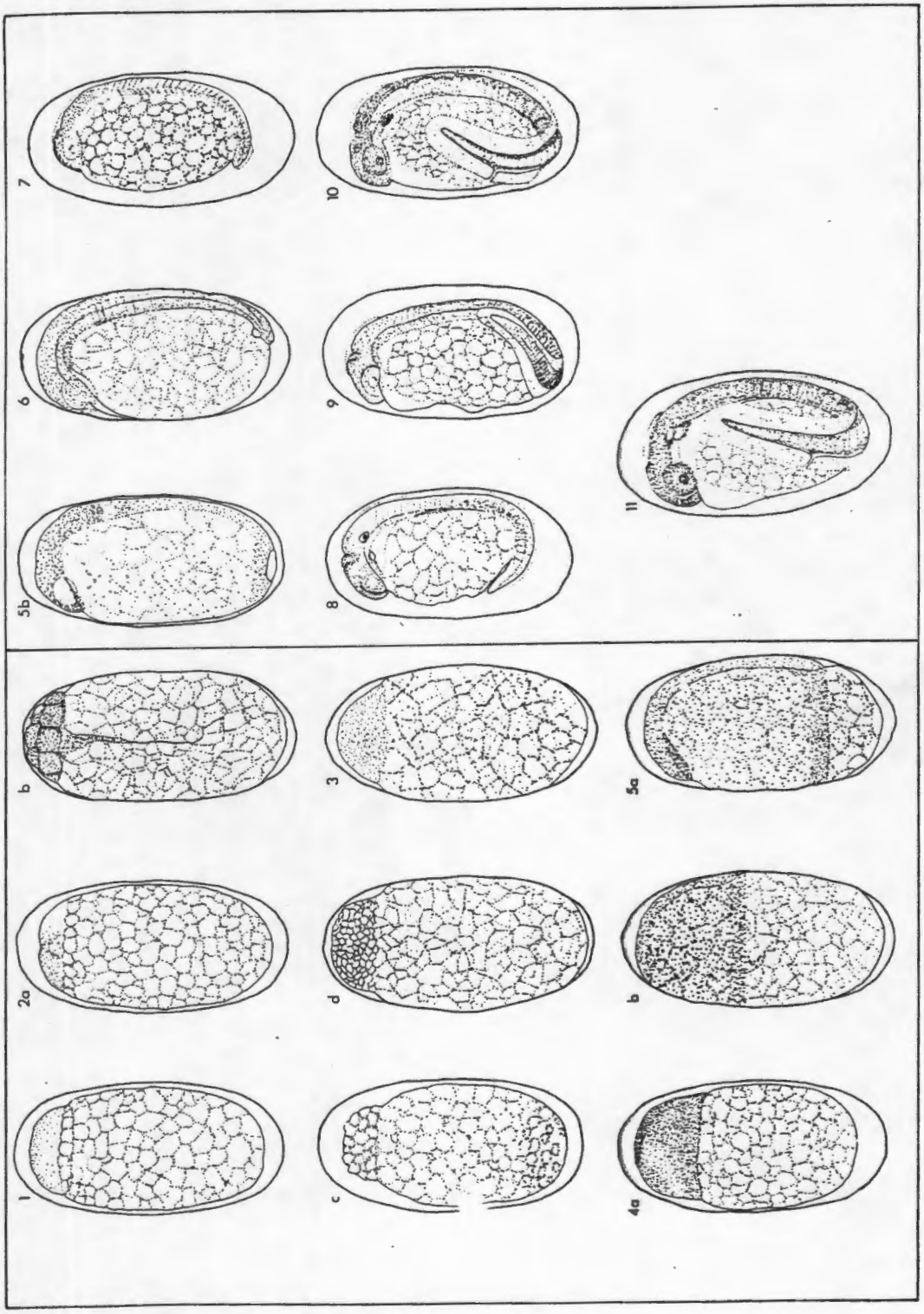


Fig. 2: Eleven developmental stages of anchovy eggs used in the determination of age for estimating rates of egg mortality (after Moser and Ahlstrom 1985)

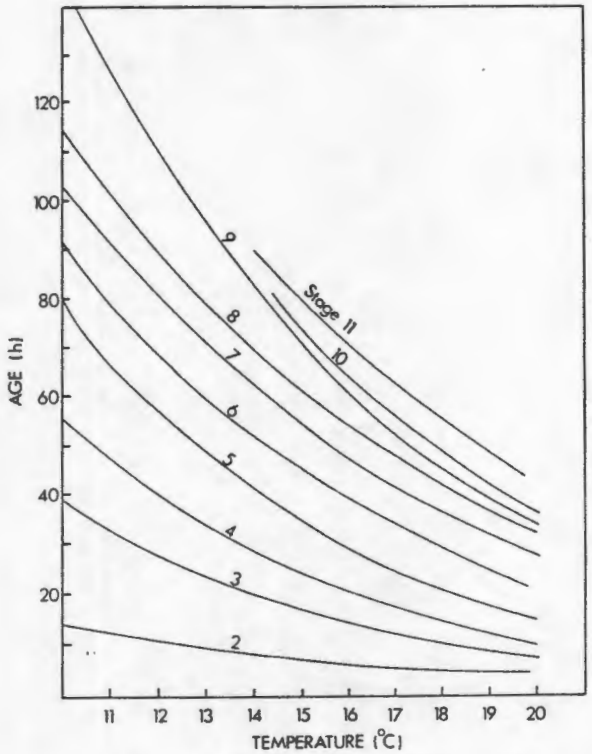


Fig. 3: Anchovy egg development curves showing the predicted mean age of the developmental stages at temperatures between 11 and 20°C

tow. A total of 40 samples was collected, and 30 fish from each sample were blast-frozen immediately after capture. In the laboratory, the fish were weighed and their stomachs were removed. The wet weights of the stomach contents were determined and the anchovy eggs in each stomach were enumerated.

RESULTS

Rates of egg mortality

The anchovy egg distribution during November 1984 and the area of intensive sampling of eggs for this study are shown in Figure 1. The abundance of eggs over the Agulhas Bank was greater than that off the West Coast, confirming that the Agulhas Bank is the major spawning area for Cape anchovy. The frequency distribution of the abundance of eggs per square metre estimated from CalVET net samples during the intensive study is shown in Figure 4. Approximately 55 per cent of the eggs was found in only 25 per cent of the samples, and the largest number collected in one haul, 12 360·m^{-2}, represented some 8 per cent of the total collected, an indication of the degree of patchiness found in egg distributions at sea. The mean density was 3 755,6 eggs·m^{-2}.

The mortality of anchovy eggs was assumed to conform to an exponential decay model (Lasker and Smith 1976) of the form

$$E_t = E_0 \cdot e^{(-Zt)} , \qquad (1)$$

where E_t is the number of eggs at age t, E_0 is the number of eggs at age 0, Z is the hourly instantaneous rate of mortality and t is the age of eggs in hours. The estimate of Z obtained by non-linear least-squares regression was 0,024·h^{-1} within the intensive sampling area in 1984 (standard error SE = 0,010). This corresponds to a survival rate to hatching of 24 per cent (Fig. 5). In comparison, the estimate of Z obtained for the whole survey grid in 1984 was 0,012 (SE = 0,007), corresponding to a survival rate to hatching of 49 per cent (SFRI, unpublished data).

Rates of egg consumption and cannibalism mortality

The frequency distribution of numbers of eggs per stomach is shown in Figure 6. Eggs were found in the stomachs of 60 per cent of the adult anchovy sampled, the mean being 19,9 (SE = 7,1) anchovy eggs per stomach. The maximum number of eggs found in a single stomach was 815, i.e. 3,5 per cent of the total number of eggs in the stomachs of all fish sampled. The daily consumption of eggs by anchovy was estimated from the mean number of eggs in the stomach during the feeding period, the duration of the feeding period and the rate of gastric evacuation. The diel pattern of feeding was examined by plotting the weight of food in the stomach, the number of eggs in the stomach, the percentage of fish without eggs in the stomach and the number of eggs in the stomach per unit mass of stomach contents against time of day (Keast and Welsh 1968, Noble 1972). The results are shown in Figure 7. Third-order polynomial regressions were fitted to the data (merely to emphasize the trends) by means of a linear least-squares method (SAS Institute Inc. 1982). The results in Figure 7a and 7d reveal a marked decrease in both weight of stomach contents and relative contribution of anchovy eggs to the stomach contents between the peak spawning period (centred around 21h00) and approximately 05h00–06h00. It is concluded, therefore, that feeding was at a minimum between 20h00–21h00 and 05h00–06h00 the following morning.

The mean number of eggs observed per stomach during the feeding period (05h00–20h00) was 36,74 (SE = 12,72). If the mean number of eggs per stomach during the feeding period and the duration

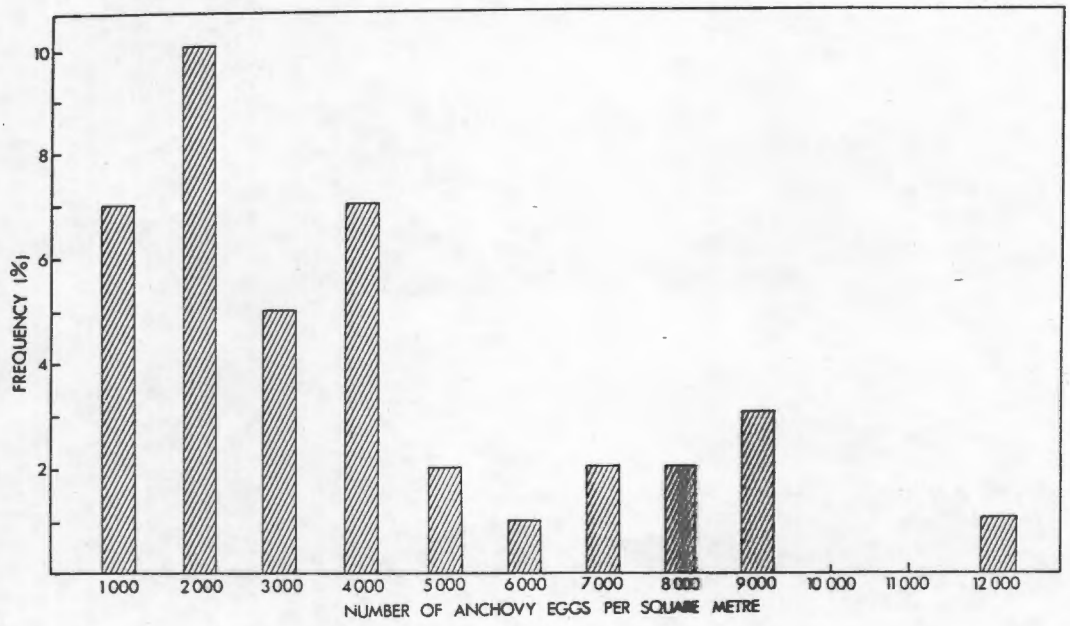


Fig. 4: Frequency distribution of anchovy egg densities

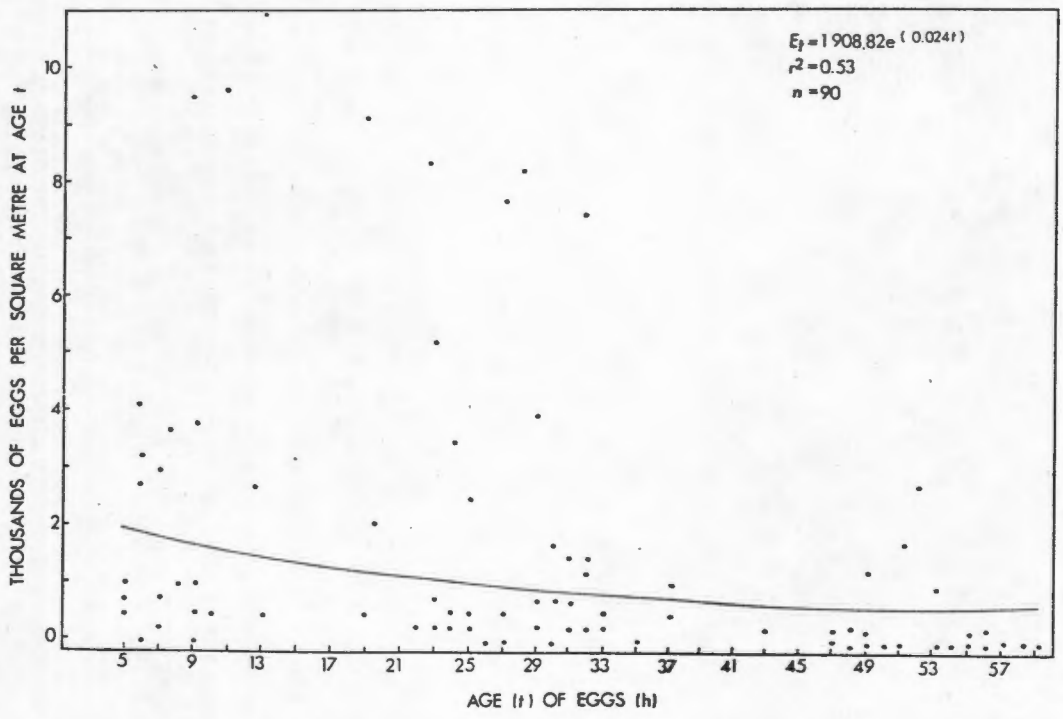


Fig. 5: Mortality curve for anchovy eggs obtained by non-linear regression of egg abundance against age. Each point represents the abundance of eggs from a spawning event that took place up to three nights prior to sampling

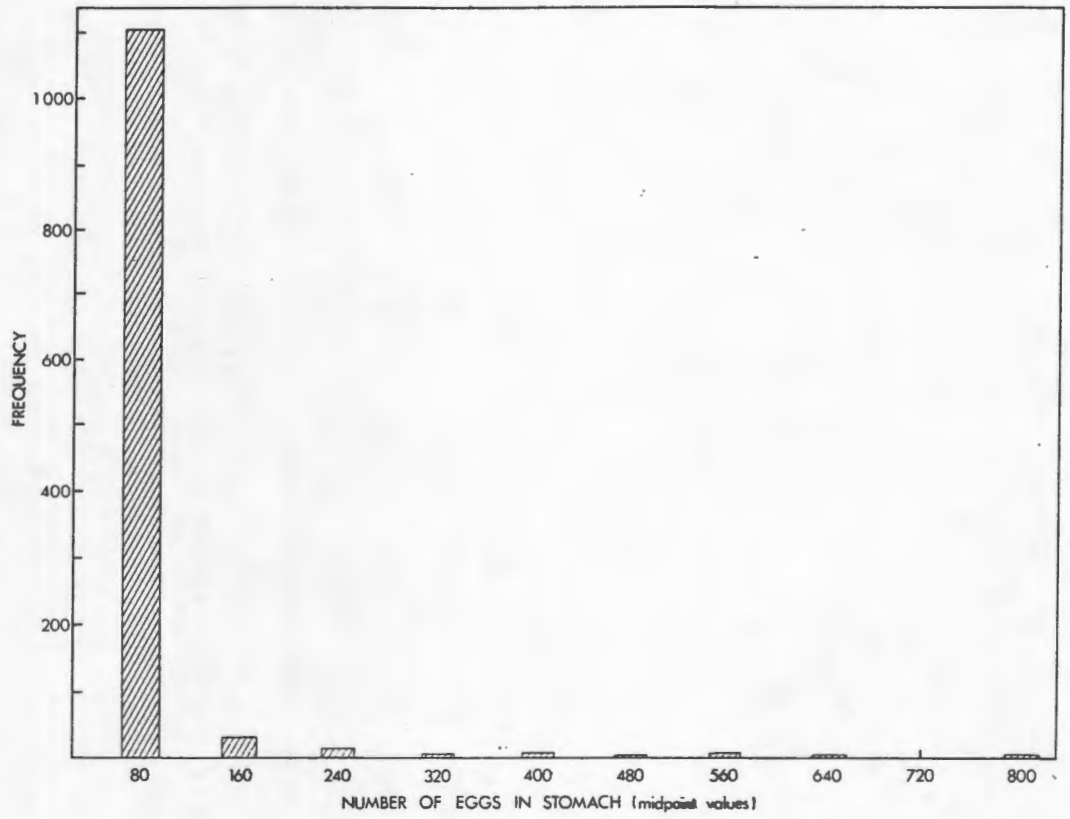


Fig. 6: Frequency distribution of numbers of eggs in the stomachs of anchovy

of feeding are considered, the average consumption of eggs during this time can be estimated (Darnell and Meierotto 1962, Tyler 1970, Noble 1972) from:

$$C = EE \,.\, g \,.\, t \quad , \qquad (2)$$

where C is the mean number of eggs eaten per fish during time t, EE is the mean number of eggs observed per stomach, t is the duration of feeding (h) and g is the rate of gut evacuation.

This equation is derived assuming a steady state between ingestion and gastric evacuation during time t. Although there was an apparent trend in egg consumption with time, Equation (2) provides a simple method for calculating the number of eggs eaten and allows the variance in egg consumption during the feeding period to be easily derived from the variance in the mean number of eggs per stomach. Feeding was therefore assumed to take place at a continuous rate over a 15-hour period, representing the average rate of egg ingestion between the times of commencement (05h00) and termination (20h00) of feeding observed during the four-day intensive study. For a more comprehensive examination of rates of egg cannibalism, it will clearly be important to establish the regularity and the magnitude of diel feeding patterns over the Agulhas Bank.

For values of $EE = 36{,}74$ and $g = 0{,}701$ (Hunter and Kimbrell 1980), the mean consumption per fish C over the period $t = 15$ h was calculated from Equation 2 as 386 eggs. As feeding was assumed to be zero between 20h00 and 05h00, this value is equivalent to the average daily intake of eggs per fish. Integration over 24 h of the polynomial expressing mean eggs per stomach as a function of time of day (Fig. 7b) gave a somewhat lower value of daily egg consumption per fish of approximately 290, emphasizing the desirability of confirming the diel feeding pattern in further studies.

The proportion of egg production consumed by cannibalism was calculated by assuming that a single day's consumption of eggs from the daily cohorts

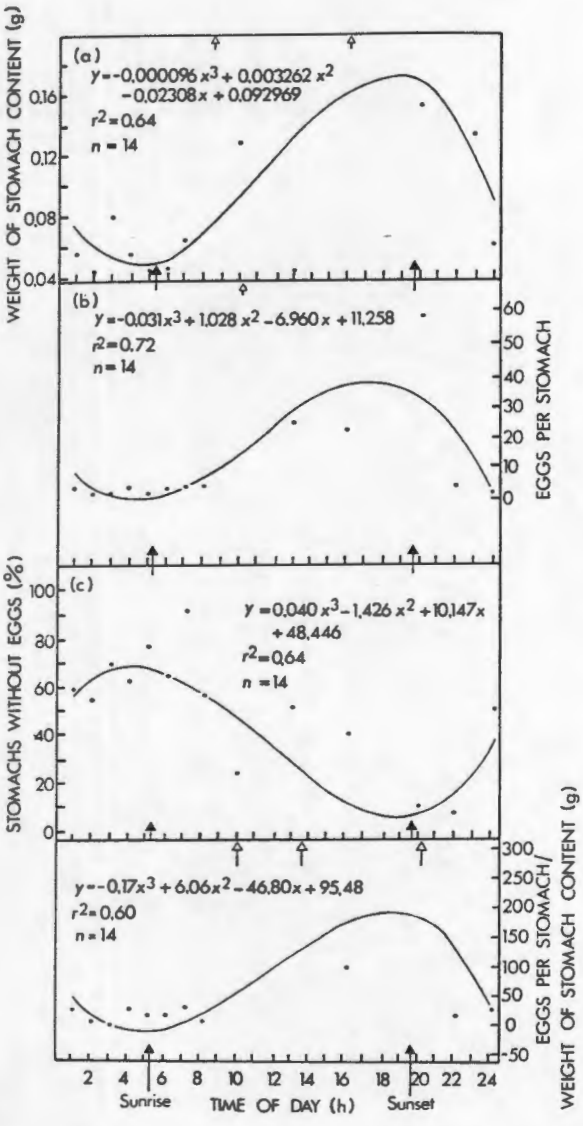


Fig. 7: Third-order polynomial model for (a) mass of stomach contents, (b) number of eggs in fish stomachs, (c) percentage of fish without eggs in the stomach and (d) number of eggs in the stomach per unit weight of stomach contents, all against time of day. Points are means for 30 fish per sample taken from 2–4 trawls and open arrows indicate points out of range of scale

produced during the preceding 2–3 days was equivalent to the consumption of eggs from a single cohort during the 2,5 days between fertilization and hatching (at 17°C). Thus:

$$Z_c = C/F\ , \qquad (3)$$

where Z_c is the proportion of egg production consumed due to cannibalism, C is the number of eggs eaten per fish per day and F is the egg production per fish per day.

$$F = f\,.\,S\,.\,r\ , \qquad (4)$$

where f is the mean number of eggs produced in a single batch by each female (batch fecundity), S is the mean proportion of females spawning each night (spawning fraction) and r is the mean ratio of mass of females to the combined mass of males, females and immature fish (sex ratio).

During the November 1984 cannibalism study, batch fecundity and spawning fraction of anchovy were estimated to be 7 772 eggs and 0,15 respectively (SFRI, unpublished data). The sex ratio of the fish sampled during the intensive study was 0,54. Therefore, the number of eggs produced per fish per day (Equation 4) was 630 and the proportion of egg production consumed by cannibalism (Equation 3) was 0,61.

The proportion of egg mortality caused by cannibalism (P_c) during the 60-h period prior to hatching was calculated as the proportion of egg production consumed due to cannibalism divided by that proportion lost due to all causes of mortality. Thus:

$$P_c = \frac{Z_c}{1 - e^{(-60\,.\,Z)}}\ , \qquad (5)$$

where all parameters are as defined in earlier equations and the denominator expresses the mortality rate over the 60-h period to hatching. The mean and the variance of P_c were estimated empirically by Monte Carlo simulation using the standard error of EE and the standard error of Z and with values of r, S, f and g assumed known precisely. A total of 3 000 values of EE and Z was generated and the mean and the standard deviation of P_c were calculated. Only positive values of EE and Z were accepted, and only values of P_c between 0 and 1,0 were included in the calculation. The mean value of P_c obtained was 0,7 (Fig. 8), and the standard error of P_c was 0,2. Therefore, cannibalism may account for 30–100 per cent (mean ± 2 SE) of the total egg mortality, with a best estimate of 70 per cent. (The daily egg consumption of approximately 290 eggs estimated by integration over 24 h of the polynomial expressing mean number of eggs per stomach as a function of time of day provided a value of 60 per cent for the proportion of total mortality attributable to cannibalism.)

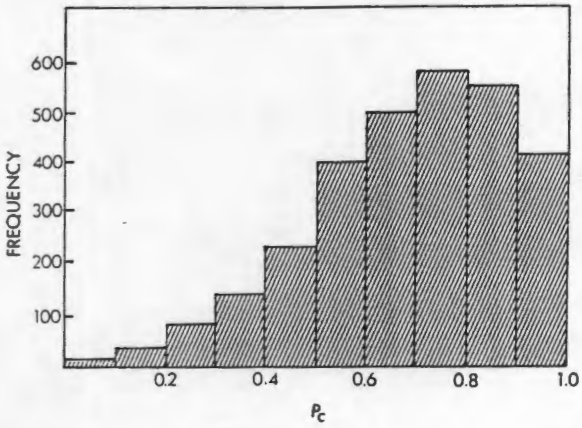


Fig. 8: Frequency distribution of the proportion of total mortality attributable to cannibalism (P_c) obtained from a Monte Carlo estimation procedure

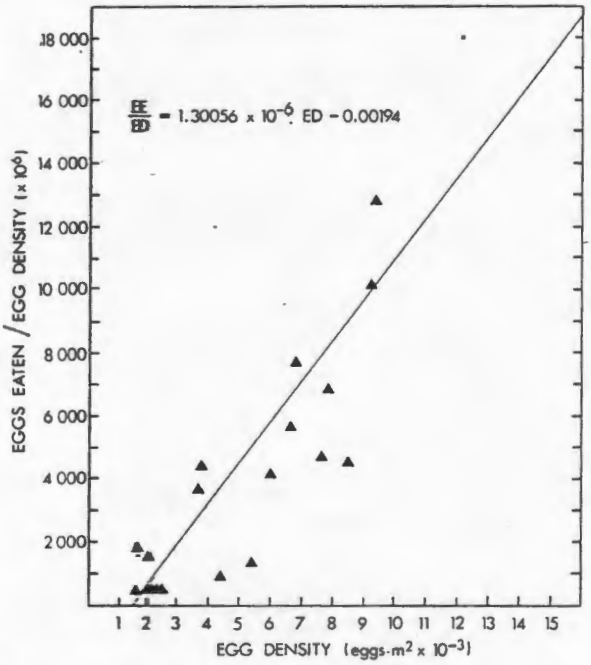


Fig. 9: Plot of the ratio of mean eggs per stomach in each trawl sample of 30 fish taken during the feeding period, to egg density, measured in the nearest CalVET net dip, against egg density. The equation for the line drawn through the data was determined by least-squares regression

The mean number of eggs observed per stomach in this study applies to an area of generally intense spawning, but egg density varied between approximately 2 000 and 12 000 eggs·m^{-2}, providing sufficient data contrast to examine the functional relationship between rate of egg consumption and egg density. An index of rate of cannibalism mortality inflicted per fish was obtained as the ratio of the mean number of eggs observed in the 30 fish stomachs at a trawl station (EE) to the estimated density of eggs from the nearest CalVET sample (ED). The ratio EE/ED was plotted against ED (Fig. 9) and linear regression parameters were estimated by least-squares. The 95-per-cent confidence limits for the estimate of the slope of regression did not include zero, and the implication of this result is that the rate of cannibalism mortality per fish varied as an increasing function of egg density within the study area.

DISCUSSION

From data in Hunter and Kimbrell (1980), MacCall (1981) estimated that cannibalism accounted for between 20 and 28 per cent of the total mortality of Californian anchovy eggs and, off Peru, Alheit (1987) attributed about 22 per cent of the total egg mortality to cannibalism. In this paper it is estimated that, on average, cannibalism accounted for 70 per cent of the total egg mortality within an area of intense spawning off South Africa. The data collected off South Africa were analysed to provide evidence that the rate of cannibalism mortality inflicted per fish varied according to egg density. Examination of the data in Figure 2 of Hunter and Kimbrell (op. cit.) reveals a similar functional response, which the authors attributed to the patchy nature of the egg distributions. They implied that, whereas the abundance of eggs in fish stomachs may be linearly related to the number of eggs per unit volume in egg patches, a curvilinear relationship may be evident if the egg densities are expressed as integrated values over the water column.

A recent investigation of vertical egg distribution by means of a plankton pump showed that anchovy egg densities over the Agulhas Bank were fairly uniform within the region of the upper mixed layer inhabited by anchovy (Shelton *et al.* in prep.). It is therefore considered here that the observed relationship may alternatively have resulted from a density-dependent response of individual fish to the abundance of eggs in their vicinity. The differences in rate of cannibalism mortality between California, Peru and South Africa could therefore have resulted from differences in egg densities found in the vicinity of the fish trawled during the three studies (the studies off California and Peru encompassed a much larger proportion of the spawning area than off South

Africa). Similarly, the large variance associated with the mean number of eggs in the stomachs (and hence the variance of the estimate of the percentage of total egg mortality that can be ascribed to cannibalism) off both South Africa (this study) and California (Hunter and Kimbrell 1980) is partly a reflection of the density-dependent response and not just measurement error.

In addition to variability in the rate of cannibalism introduced by a density-dependent predator-prey response, the rate of cannibalism is likely to depend on the size, abundance and distribution of adult food in the spawning area. For example, anchovy could be expected to ingest more eggs in an area where particles other than anchovy eggs were rare in the plankton than in an area with the same density of anchovy eggs, but a greater density of other plankton particles. The time spent filter-feeding (when eggs are ingested — Hunter and Kimbrell 1980) as opposed to particulate feeding will depend on the relative abundances of different sizes and types of prey organism. This will tend to obscure the underlying functional response, but it may be resolved by more detailed examination of the stomach contents and the plankton in future studies.

The impact of cannibalism as a density-dependent mechanism influencing the survival of eggs to hatching will therefore vary according to the pattern of fish density, specific fecundity (dependent on sex ratio, fecundity and spawning fraction) and abundance of planktonic food over the spawning grounds and within the spawning season. These aspects will be considered in a subsequent publication (Valdés *et al.* in prep.) in which a model is developed to relate the numbers of eggs hatching to the number of eggs produced by anchovy.

ACKNOWLEDGEMENTS

We wish to express our thanks and appreciation to Dr J. Alheit (Alfred-Wegener-Institute for Polar and Marine Research, Bremerhaven, Germany) and to Dr M. O. Bergh (University of Cape Town), for their helpful comments. We also thank the Director of the Sea Fisheries Research Institute for support and for permission to use the project for an M.Sc. dissertation by the first author.

LITERATURE CITED

ALHEIT, J. 1987 — Egg cannibalism versus egg predation: their significance in anchovies. In *The Benguela and Comparable Ecosystems.* Payne, A. I. L., Gulland, J. A. and K. H. Brink (Eds). *S. Afr. J. mar. Sci.* 5: 467–470.

BLAXTER, J. H. S. and J. R. HUNTER 1982 — The biology of the clupeoid fishes. *Adv. mar. Biol.* 20: 1–398.

DARNELL, R. M. and R. R. MEIEROTTO 1962 — Determination of feeding chronology in fishes. *Trans. Am. Fish. Soc.* 91(3): 313–320.

DE CIECHOMSKI, J. D. 1967 — Investigations of food and feeding habits of larvae and juveniles of the Argentine anchovy *Engraulis anchoita. Rep. Calif. coop. oceanic Fish. Invest.* 11: 72–81.

DE CIECHOMSKI, J. D. and C. I. BOOMAN 1982 — Distribución cuantitativa de huevos y larvas de anchoita (*Engraulis anchoita*) en la plataforma continental, frente a las costas de la Argentina y Uruguay en el ciclo anual 1981/1982. *Contrn Inst. nac. Invest. Pesq.* 431: 1–4.

HAMPTON, I., SHELTON, P. A. and M. J. ARMSTRONG 1985 — Direct estimates of anchovy spawner biomass off SA. *S. Afr. Shipp. News Fishg Ind. Rev.* 40(4): 31, 33.

HAYASI, S. 1967 — A note on the biology and fishery of the Japanese anchovy *Engraulis japonica* (Houttuyn). *Rep. Calif. coop. oceanic Fish. Invest.* 11: 44–57.

HETTLER, W. F. 1976 — Influence of temperature and salinity on routine metabolic rate and growth of young Atlantic menhaden. *J. Fish Biol.* 8: 55–65.

HOLANOV, S. H. and J. C. TASH 1978 — Particulate and filter feeding in threadfin shad, *Dorosoma petenense*, at different light intensities. *J. Fish Biol.* 13: 619–625.

HUNTER, J. R. and C. A. KIMBRELL 1980 — Egg cannibalism in the northern anchovy, *Engraulis mordax. Fishery Bull., Wash.* 78(3): 811–816.

KEAST, A. and L. WELSH 1968 — Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. *J. Fish. Res. Bd Can.* 25(6): 1133–1144.

KING, D. P. F. 1977 — Influence of temperature, dissolved oxygen and salinity on incubation and early larval development of the South West African pilchard *Sardinops ocellata. Investl Rep. Sea Fish. Brch S. Afr.* 114: 35 pp.

KING, D. P. F., ROBERTSON, A. A. and P. A. SHELTON 1978 — Laboratory observations on the early development of the anchovy *Engraulis capensis* from the Cape Peninsula. *Fish. Bull. S. Afr.* 10: 37–45.

LASKER, R. 1975 — Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. *Fishery Bull., Wash.* 73(3): 453–462.

LASKER, R. 1985 — What limits clupeoid production? *Can. J. Fish. aquat. Sci.* 42(Suppl. 1): 31–38.

LASKER, R. and A. MacCALL 1983 — New ideas on the fluctuations of the clupeoid stocks off California. In *Proceedings of the Joint Oceanographic Assembly 1982: General Symposia.* Ottawa; Canadian National Committee/Scientific Committee on Oceanic Research: 110–120.

LASKER, R. and P. E. SMITH 1976 — Estimation of the effects of environmental variations on the eggs and larvae of the northern anchovy. *Rep. Calif. coop. oceanic Fish. Invest.* 19: 128–137.

LOUKASHKIN, A. S. 1970 — On the diet and feeding behavior of the northern anchovy, *Engraulis mordax* (Girard). *Proc. Calif. acad. Sci, Ser. 4* 437(13): 419–458.

MacCALL, A. D. 1981 — The consequences of cannibalism in the stock-recruitment relationship of planktivorous pelagic fishes such as *Engraulis.* In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, 1980.* Sharp, G. D. (Conv. Ed.). Paris; Unesco: 201–228. (*I.O.C. Workshop Rep.* 28).

MOSER, H. G. and E. H. AHLSTROM 1985 — Staging anchovy eggs. In *An Egg Production Method for Estimating*

Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, Engraulis mordax. Lasker, R. (Ed.). *Tech. Rep. NOAA NMFS* 36: 37–41.

MURPHY, G. I. 1977 — Clupeoids. In *Fish Population Dynamics*. Gulland, J. A. (Ed.). New York; Wiley-Interscience: 283–308.

NOBLE, R. L. 1972 — A method of direct estimation of total food consumption with application to young yellow perch. *Progve Fish-Cult.* 34(4): 191–194.

O'CONNELL, C. P. 1972 — The interrelation of biting and filtering in the feeding activity of the northern anchovy (*Engraulis mordax*). *J. Fish. Res. Bd Can.* 29: 285–293.

ROJAS DE MENDIOLA, B. 1981 — Summary of the studies about food and feeding habits of the anchovy (*Engraulis ringens* J.). In *Report and Supporting Documentation of the Workshop on the Effects of Environmental Variation on the Survival of Larval Pelagic Fishes, Lima, 1980*. Sharp, G. D. (Conv. Ed.). Paris; Unesco: 221–231 (*I.O.C. Workshop Rep.* 28).

ROJAS DE MENDIOLA, B. and N. OCHOA 1973 — Observations on the food and feeding habits of the anchovy *Engraulis ringens* Jenyns made during cruise 6908–09. In *Oceanography of the South Pacific*. Fraser, R. (Comp.). Wellington, New Zealand; New Zealand National Commission of UNESCO: 457–461.

ROJAS DE MENDIOLA, B., OCHOA, N., CALIENES, R. and O. GÓMEZ 1969 — Contenido estomacal de anchoveta en cuatro áreas de la costa peruana. *Infme Inst. Mar Perú* 27: 29 pp.

SANTANDER, H., ALHEIT, J., MacCALL, A. D. and A. ALAMO 1983 — Egg mortality of the Peruvian anchovy (*Engraulis ringens*) caused by cannibalism and predation by sardines (*Sardinops sagax*). In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* 291(3): 1012–1025.

SANTANDER, H., ALHEIT, J. and P. E. SMITH 1984 — Estimación de la biomasa de la población desovante de anchoveta peruana *Engraulis ringens* en 1981 por aplicación del "Metodo de Producción de Huevos". *Boln Inst. Mar Perú* 8(6): 209–250.

SAS INSTITUTE INC. 1982 — *SAS User's Guide: Statistics*. Cary, North Carolina; SAS Institute Inc.: 584 pp.

SHELTON, P. A. 1986 — Fish spawning strategies in the variable southern Benguela Current region. Ph.D. thesis. University of Cape Town, Cape Town: [vi] + 327 pp.

SHELTON, P. A. and M. J. ARMSTRONG 1983 — Variations in parent stock and recruitment of pilchard and anchovy populations in the southern Benguela system. In *Proceedings of the Expert Consultation to Examine Changes in Abundance and Species Composition of Neritic Fish Resources, San José, Costa Rica, April 1983*. Sharp, G. D. and J. Csirke (Eds). *F.A.O. Fish. Rep.* 291(3): 1113–1132.

SHELTON, P. A. and L. HUTCHINGS 1981 — The effect of the environment on spawning and recruitment in the anchovy (*Engraulis capensis* Gilchrist). *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 178: 202–203.

SHELTON, P. A. and L. HUTCHINGS 1982 — Transport of anchovy, *Engraulis capensis* Gilchrist, eggs and early larvae by a frontal jet current. *J. Cons. perm. int. Explor. Mer* 40(2): 185–198.

SHELTON, P. A., HUTCHINGS, L., HAMPTON, I. and M. J. ARMSTRONG (in preparation) — Anchovy spawning in the southern Benguela.

SMITH, P. E. 1985 — Year-class strength and survival of O-group clupeoids. *Can. J. Fish. aquat. Sci.* 42(Suppl. 1): 69–82.

SMITH, P. E., FLERX, W. and R. P. HEWITT 1985 — The CalCOFI vertical egg tow (CalVET) net. In *An Egg Production Method for Estimating Spawning Biomass of Pelagic Fish: Application to the Northern Anchovy, Engraulis mordax*. Lasker, R. (Ed.). *Tech. Rep. NOAA NMFS* 36: 27–32.

SMITH, P. E. and R. LASKER 1978 — Position of larval fish in an ecosystem. *Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer* 173: 77–84.

STAUFFER, G. D. and S. J. PICQUELLE 1980 — Estimates of the 1980 spawning biomass of the central subpopulation of the northern anchovy. *Admin. Rep. SW. Fish. Cent., La Jolla* LC-80-09: 24 pp. + 3 Tables + 15 Figures.

TYLER, A. V. 1970 — Rates of gastric emptying in young cod. *J. Fish. Res. Bd Can.* 27: 1177–1189.

VALDÉS, E. S., SHELTON, P. A., ARMSTRONG, M. J. and J. G. FIELD (in preparation) — Egg cannibalism in South African anchovy: functional response.